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BULLETIN
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THE STRUCTURE AND DEVELOPMENT OF OPHIOGLOSSUM PALMATUM

M. A. CHRYSLER[1]

(WITH TWENTY-ONE FIGURES)

Ever since its discovery in Hispaniola by Plumier early in the eighteenth century *Ophioglossum palmatum* L. has attracted attention, partly because of its unusual form and partly no doubt because of its rarity. In the original description of the plant Plumier (1705) says: "Je n'ay jamais rencontré cette plante qu'une seule fois, dans tous mes trois voyages dans les Isles de l'Amérique." Considering the general rarity of the plant, it comes as a matter of surprise to read in a letter from the late Dr. J. K. Small: "Forty or fifty years years ago one could go to the edge of the Everglades back of Miami (Florida) and collect it by the wagon load. Today not a leaf can be found there."

MATERIAL AND METHODS

Through Doctor Small's kindness material was preserved in the field during one of his last visits to Florida, namely in November 1936. In order to secure a series of stages in development, I visited one of the Florida stations in January 1938, on which occasion I was favored by the cooperation of Dr. H. H. Hume and Mr. Erdman West, both of the Florida Agricultural Experiment Station, also of Dr. E. P. St. John and Dr. R. P. St. John. Hearty thanks are here extended to these botanists, especially for providing the ladders which were necessary to enable one to dislodge the plants from their position in the decaying matter beneath the crowns of the palmettoes, *Sabal Palmetto* (Walt.) Todd, in company with *Polypodium aureum* L. and *Vittaria lineata* (L.) Sw. A second visit to the same station was made in April 1939, on which occasion I had the help of Professor M. A. Johnson of Rutgers University as well as of the St. John brothers. On these occasions an effort was made to secure gametophytes, but unfortunately without success. Even the young sporophytes appear to have arisen as buds from roots of older plants (v. Bower 1911).

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[1] Publication of Bureau of Biological Research, Rutgers University.

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Most of the material was fixed in formalin-acetic-alcohol, but for the young spikes Allen's modification (''PFA^3'') of Bouin was used. For staining developing sporangia iron alum haematoxylin followed by gold orange proved to be entirely satisfactory, although in some cases the safranin-fast green combination was used. Picro-aniline blue seemed to be on the whole the most suitable stain for the mycorrhizae. Methods for clearing leaves proved to be of small value in tracing the course of the vascular bundles—even series of sections cut freehand and mounted in glycerine gave superior results.

In addition to the microscopic study a survey of the superficial features has been made of the numerous specimens represented in the herbaria at Kew, the British Museum, and the New York Botanical Garden. An examination of all available illustrations of the plant leads to the conclusion that many of them are distinctly unsatisfactory in their attempt to display the critical features.

The objects of the present study have been to find to what extent development in this species (genus?) differs from that of members of the group *Euophioglossum;* to examine in a sufficient number of individuals the attachment of the fertile spikes; and to attempt a revaluation of the different theories which have been proposed as to the morphological nature of the spike.

The earliest work on the internal structure of this plant appears to have been by Bertrand and Cornaille (1902), who figure a section through a leaf-stalk. In 1904 Bower was able from a Jamaica specimen to trace the origin of the vascular strands which supply the spikes. These results were confirmed and an analysis of the stem structure was made in 1911, when he had access to another plant from the same source. This work was supplemented by careful study of many herbarium sheets. At about the same time Campbell (1911) in his work on the Eusporangiatae made brief reference to certain features of root and leaf. Apparently no material was available to the previous workers for study of the development of sporangia and spores.

THE ROOT

The roots—all adventitious in the mature plant—are numerous and may reach a length of 240 mm., with diameter from 1.5 to 2 mm., penetrating the loose litter between the dead leaf bases of the palmetto, as we find the plant growing in Florida. Occasional branchings which are to be regarded as dichotomies occur. The absence of root-hairs is in keeping with the mycorrhizal habit. At a short distance back of the region covered by the root-cap it is seen that the outer layer of the root, which would ordinarily be developed as a piliferous layer, comes to have a firm wall which is impregnated with a highly impervious substance which stains with safranin, but does not yield reactions for lignin or suberin. The outer wall of the cells in question is especially thickened in older regions of a root, and may assume a yellow color. With this may be compared the observations of Petry (1914) on the root of *O. pendulum*. The general features of the mature root are represented in figures 5, 17, in which it may be made out that the external layer of cells is followed by an outer cortex devoid of intercellular spaces and having a thickness of from five to seven cells. These cells have a transverse diameter of about 70 μ and a length of about 300 μ; they contain numerous very small starch grains, and the inner part of the layer (2–3 cells thick) may contain a fungus. The inner cortex has a thickness of 4–5 cell diameters and its cells display a thickening which approaches collenchyma; where three cells meet the walls are markedly thickened and the secondary wall stains like cellulose, while the primary wall is well developed in the "corner" regions, taking a strong safranin stain. But in the innermost parts of the cortex the primary wall disappears, leaving the usual triangular intercellular spaces. The endodermis displays a plain Caspary's band. The stele has an average diameter of about 0.4 mm., and shows a continuous mass of xylem which is diarch in a large majority of the roots which have been examined, although, as noted by Campbell (1911), the triarch condition also occurs, and both the diarch and triarch condition is to be seen in different roots of the same plant. Moreover a triarch root may distally become diarch, especially after a dichotomy. A section through the stele of one of the triarch roots is shown in figure 5. With this may be contrasted the stele of *O. fibrosum*, figured by Maheshwari and Singh (1934), in which species the three xylem groups are widely separated.

Mycorrhiza. The occurrence of a fungus in the outer cortical layer has already been mentioned, and is conspicuous when present. Bower (1911) refers to "the presence of endotrophic mycorrhiza, though not in such profuse development as the habit of the plant might lead one to expect." Many root sections fail to show fungi, even at a distance of some centimeters from the tip. Moreover the mycorrhizal zone may extend only part way around the root, indicating a local infection. In the Florida material very few cells containing filamentous hyphae ("fungus host cells") have been found, but most have passed into the digestive stage, i.e., they show irregular lumps of varying size and shape occupying a large part of the cell, not however including the nucleus. Coenocytic hyphae but no reproductive cells have been observed, so it would not be possible to identify the fungus as *Stigeosporium Marattiacearum*. In this action we thus follow Burgeff (1938) in his discussion of the mycorrhizae of *O. pendulum*.

The tip region of the root cut in longitudinal and transverse planes shows a tetrahedral apical cell with four cutting faces, and is thus typical of the order (Bower 1926). Mitoses in adjoining cells are frequent, indicating that growth was rapid in the early spring period in which the material was collected. The mitotic figures contain a very large number of small narrow chromosomes, and could not be counted in this part of the plant (*vide infra*). No irregular segmentation similar to that observed in *O. pendulum* by Petry (1914), and by him attributed to slow growth, were found in the Florida material. Differentiation of the xylem within 4 mm. of the tip was found in two of the roots. This xylem already displayed the type of tertiary thickening which is characteristic of the tracheids in Ophioglossales.

THE STEM

The rhizome has a definitely stocky form in the Florida specimens, mature individuals having an average diameter of 9 mm. and a length approximately the same. Bower gives the diameter of his Jamaica specimen as ¾ inch, which appears to be rather above the average. Moreover the Florida plants usually show from three to four functional leaves at one time instead of the single one which is represented in some herbarium specimens.

Judging from the number of withered leaf bases surrounding the larger rhizomes, and from the prevalence of smaller plants, growth of the stem is slow. This results in a crowding of the leaves, involving complexity of the vascular skeleton. Bower succeeded in resolving the network into a fairly narrow dictyostele in which the vascular supply of a leaf arises as two strands, one from each side of a wide gap. A quite peculiar condition exists in the form of a "commissure" stretching between the two strands immediately above the point of exit from the stele. I have been able to confirm the foregoing as a general statement; but examination of a larger number of rhizomes indicates that the plan is subject to variation. For example, the commissure may fail to appear in some of the gaps; a root may or may not arise from the commissure; roots in some cases strike downward through the pith instead of the cortex; the double leaf trace may extend through the cortex and petiole without branching for a much greater distance than is shown in Bower's figure 4 (1911); a diarch root may lie beside a triarch one. These variations well match the wide differences in number of lobes and of fertile spikes which different individuals show.

The bundles which constitute the stele are ectophloic, with protoxylem ill-defined but mostly endarch. Secondary growth is lacking. The tracheids have the exceptional combination of spirals and pits which is characteristic of Ophioglossales (Loughridge 1932). In the position of an external endodermis some individuals have a layer whose cells are filled with dark-staining fine granules, while other individuals have some cells of the layer thick-walled, reticulate, and taking a definite stain with safranin. But in other stems no endodermis can be distinguished, and in none has a typical Caspary's band been seen. Perhaps the specialized layer should be regarded as pericycle. No fungal hyphae have been observed in any of the rhizomes, but in some cases starch grains are abundant, although they may be entirely absent from a rhizome.

THE LEAF

The branching of the sterile segment of the leaf has won for the plant the common name "hand fern" (Plumier, l.c., says "à peu prés comme une main ouverte," as well as the specific designation *palmatum*. These words, however, appear to misrepresent the true nature of the lobing. Bitter (1900) refers to "2–3 fachen Dichotomien," and this feature was first brought to my attention by inspection of several specimens in the Herbarium of the New York Botanical Garden. These plants were collected in Sta. Catharina, Brazil, and very clearly show the sterile part of the leaf twice dichotomous, with ribbon-shaped lobes. I have not been able to inspect Plumier's type specimen, but his illustration (l.c., pl. 163) shows two plants each with four nearly equal lobes, so we may infer that his specimens did not suggest dichotomy. Hooker, who had access to specimens from Mauritius, seems to have had shadowy ideas on the critical features, for his plate IV (1836) does not bring out the dichotomy and fails to indicate clearly the region of insertion of the five fertile spikes. The figure of Martius (1859, pl. 9) is much more satisfactory, showing ten fertile spikes, all marginal except the lowest, and the sterile segment twice dichotomous. Plate 7 of Bower's *Studies* (1896)

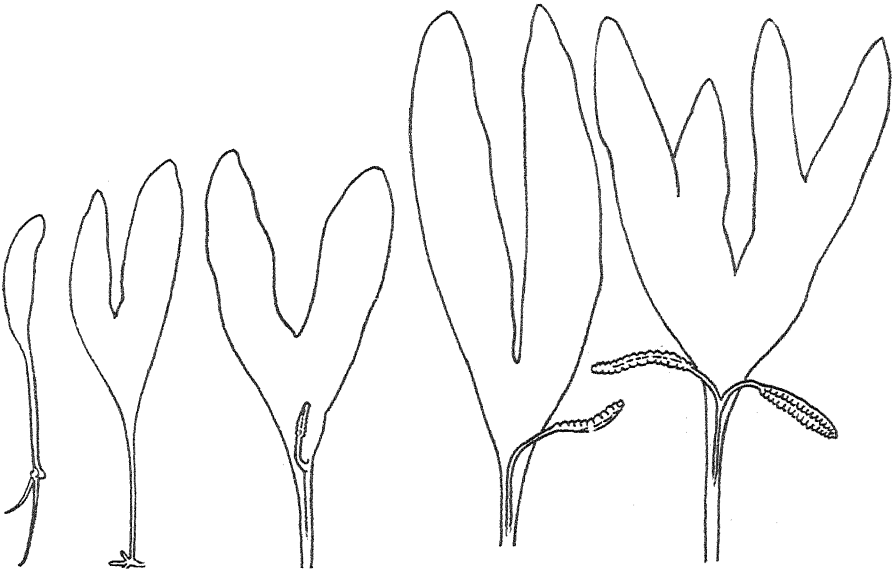
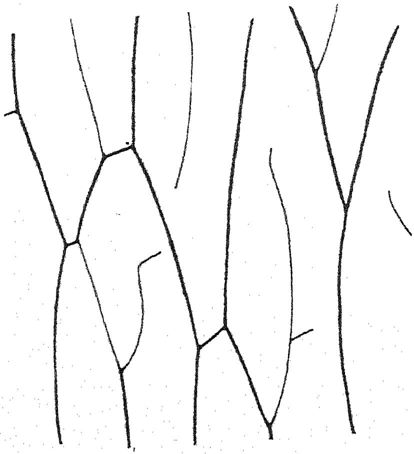


FIG. 1. Leaves showing stages in dichotomy. The two youngest leaves are sterile; the third leaf shows the unusual condition of a single marginal spike.

shows two plants with dichotomous branching, but the author appears at the time of writing not to have been impressed by the fundamental nature of dichotomy in pteridophytes, for he merely mentions (p. 29) with regard to the specimen "in fig. 118, four lobes of the sterile (two incompletely separate), and two fertile spikes." Clausen (1938) uses the expression "palmately lobed or divided," which of course expresses the form of many leaves, but gives no hint as to the real nature of the lobing. It will readily be seen that unequal development of the lobes or sinuses of a twice dichotomous blade would produce the more or less palmate effect presented by the majority of specimens. That the plan of the leaf in *O. palmatum* is inherently dichotomous is rendered probable also by the venation, which is plainly reticulate (fig. 2), but has not departed as widely from the dichotomous type as is the case in some other species, e.g., *O. Engelmanni* Prantl. It may be observed from figure 2 that in *O. palmatum* the meshes are relatively elongated, and the secondary network within the primary meshes poorly developed. Observation of young plants (fig. 1) shows the first leaf undivided and sterile, later leaves 2-lobed and either sterile or fertile, while still later leaves are more or less clearly twice dichotomous and fertile, with an increasing number of lobes and of spikes.

As seen in transverse section, the blade of the sterile segment has a thickness of about 0.5 mm., with no differentiation of a palisade. A cuticle is moderately developed, and small stomata are frequent on the lower surface. The vascular bundles are small and of the ordinary collateral type.

In the leaf-stalk, the epidermis, while only moderately thick-walled, is quite resistant to diffusion of aqueous fluids. The ground tissue is thin-



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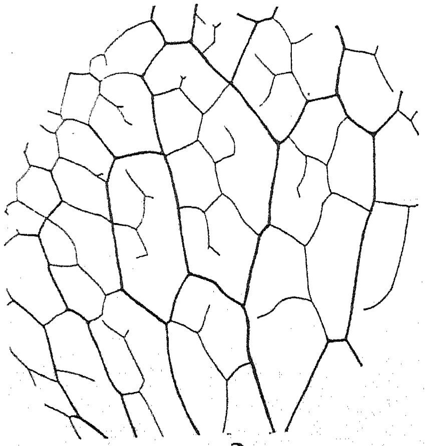

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FIG. 2. Plan of venation in leaf of *O. palmatum*. FIG. 3. Plan of venation in *O. Engelmanni*. In this species the secondary reticulum is well developed. Both × 5.

walled and undifferentiated, with cells devoid of starch. The number of vascular strands ranges from two at the base to twelve or more further up. The course of these has been clearly traced by Bower (1911, figs. 17–20) who makes the point that the strands not only increase in number upward, but anastomose and form a broad C-shaped group with the opening directed adaxially. In the upper part of the petiole the group closes so as to form a practically complete circular ring of bundles, although this is somewhat flattened adaxially in agreement with the shape of the petiole. I have been able to fully verify these observations by means of series through a number of petioles. The bundles are collateral and for the most part have endarch xylem. Larger bundles with distinctly mesarch structure are also found (fig. 6), having the protoxylem nearer the adaxial side. The tracheids of the metaxylem have the same type of thickening as is found in the stem. Shortly before petiole merges into blade, several bundles branch off from the adaxial side of the ring and curve adaxially to supply the lowest fertile spike. In agreement with Bower I fail to identify these bundles with the ones which close up the "C" into an "O," because several anastomoses have occurred at this position; all that can be said is that the strands in question arise from the region of junction of the edges of the C, and that after their departure the C-form is resumed.

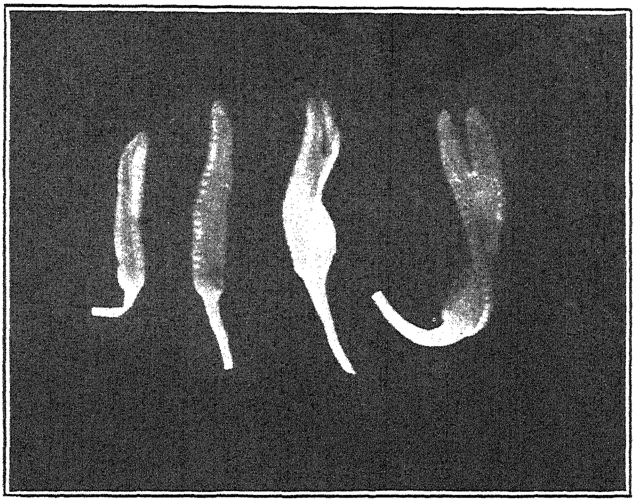

Fig. 4. Fertile spikes, all but the left-hand one abnormal.

An example of the rare cases in which there are two basal spikes in place of one (see pl. 22 in Bower 1911) has also been examined in a series of sections. The only difference from the normal is that from the adaxial group of petiolar bundles seven, lying side by side, separate slightly into a set of four and one of three bundles, each of the sets supplying one of the contiguous spikes, and leaving the petiole with a C-shaped vascular supply. Very rarely cases occur where the stalk in median position forks and gives rise to two spikes. In all the plants which have come under my observation, the vascular supply of the higher spikes arises as one or more bundles from the margin of the C, exactly as figured by Bower (1911, figs. 17–20).

Since in his paper of 1911 Bower has gone to some pains to establish the thesis that, with the exception of the lowest spike, "the insertion of the rest is usually intra-marginal" (p. 295), I have examined a considerable quantity of the Florida material to test the validity of this view. The plants in question had been preserved in liquid, and were cut free-hand into a series of sections which were mounted in glycerin. From a study of this material I can say that the uniform position of the upper spikes is marginal. It is necessary here to define what to my mind constitutes "marginal," and I have no hesitation in deciding this on the basis of vascular connection. To be explicit, I regard a spike as marginal when its vascular supply arises from the margin of the vascular system of the leaf. Bower's figures 17–20 in the paper of 1911 admirably illustrate the definition. If the vascular anatomy cannot be relied on to settle so simple a point as this, I fail to see much occasion for introducing anatomical evidence. For this reason I cannot see the significance (I do not question the accuracy) of Bower's figures 7–10, which are used to validate the statement (1911, p. 283) "whatever the vascular connections may be, the spikes of *O. palmatum* are in their prime origin intra-marginal."

As far as the mature spikes are concerned, there is a decided advantage in having access to material preserved in liquid, for the spikes are frequently decurrent to a marked degree, the stalk of a spike forming a distinct ridge upon the surface of the leaf. In a herbarium specimen this feature is apt not to be apparent, and the vascular system of a spike may be inserted on that of the leaf at a point some millimeters below the level where the stalk joins the surface of the petiole. In other words, the lower part of the stalk of a spike is in such cases fused with the petiole just as the basal part of the filament of a stamen may be fused with the surface of a corolla. In both cases

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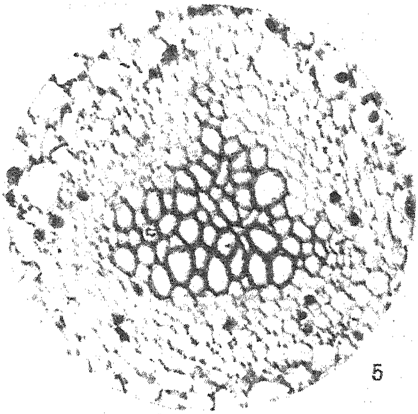
Explanation of figures 5–14

FIG. 5. Stele of triarch root. × 100. FIG. 6. Mesarch bundle from petiole. × 240. FIG. 7. Nucleus of tapetal cell in metaphase. × 250. FIG. 8. Two dividing nuclei in cell of tapetum. × 250. FIG. 9. Heteroploid nucleus of tapetal cell in metaphase. × 400. FIG. 10. Abnormal mitosis of tapetal cell. × 600. FIG. 11. Incompletely divided nucleus in tapetal cell. × 400. FIG. 12. Tapetal plasmodium with nuclei, also dividing sporocytes. × 275. FIG. 13. General view of sporangium showing the apparent wall, tapetum with several binucleate cells, sporogenous cells in various stages in different "blocks." × 95. FIG. 14. Diakinesis in sporocytes. × 525.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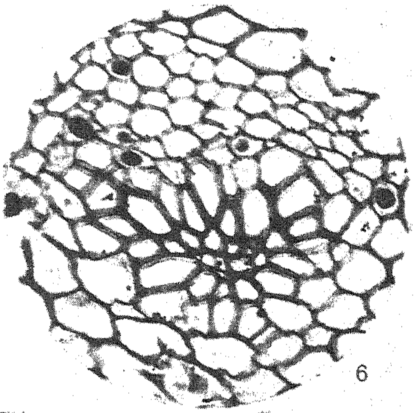
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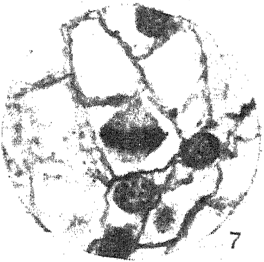
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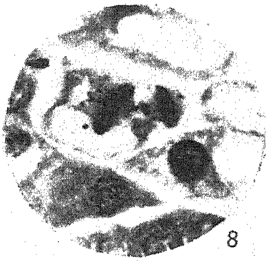
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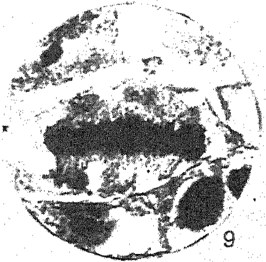
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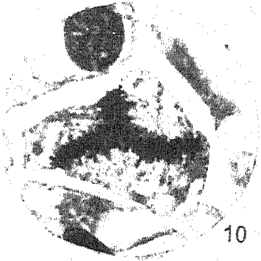
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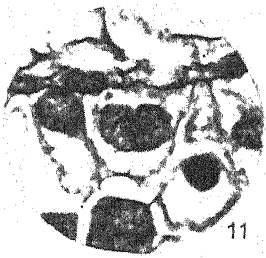
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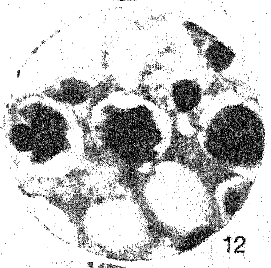
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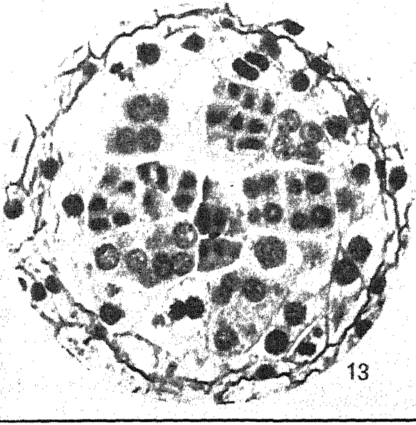
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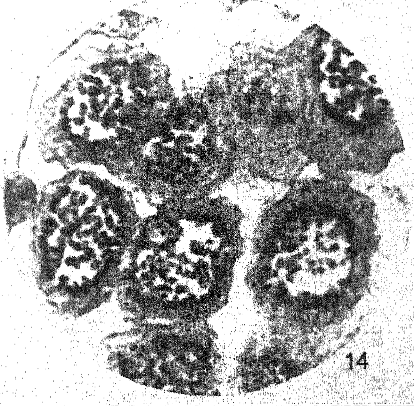
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such fusion is to be regarded as a subsequent occurrence. The Florida material shows numerous cases where one or more of the upper spikes are inserted at a point at last 3 mm. inward from the edge of the leaf in the region where leaf-stalk widens into blade; when the vascular bundles of such spikes are traced downward they invariably join an edge of the C-shaped system of the petiole, which at this level has flattened out more or less. In view of the uniformity displayed by this preserved material, it is suggested that the specimens shown in Bower's figures 120 and 121 (1896), having an unusually large number of spikes irregularly placed, may represent abnormalities.

STRUCTURE OF THE FERTILE SPIKE

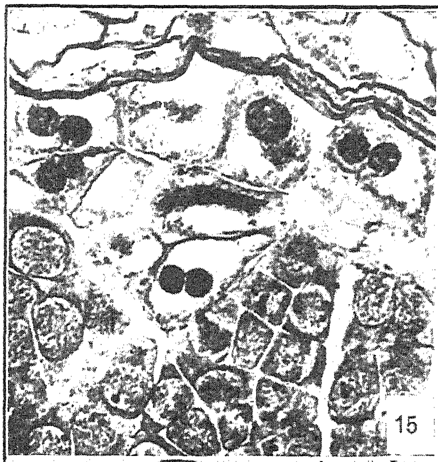
The general features of these rather large organs (30–40 mm. long and 5 mm. wide) are well known. There appears to be no constant difference between the spikes which are attached in the median adaxial region and those which arise toward the margin. The number of bundles at a level not more than 2 mm. above the point of attachment of the spike varies from one to three in the lateral spikes, and from two to four or occasionally five in median spikes. As the spore-bearing part of the spike is reached, a central bundle is found, with a slender bundle on each side, toward the sporangia. Numerous anastomoses occur between the bundles, and small branches are given off right and left into the spaces between the sporangia. When mature these organs have a diameter of ca. 1 mm., and are deeply infolded on the side toward the axis of the spike, so that their shape is distinctly reniform.

The most extensive contributions on spore development in the group have been made by Beer (1906), Cardiff (1905), and Stevens (1905).

DEVELOPMENT OF THE SPORANGIUM

The youngest fertile spikes represented in my material have a length of 2–3 mm. and a diameter up to 0.4 mm. The scanty material indicates that the apical cell is a pyramid with four cutting faces. A short distance below the apex is a somewhat indefinite indication of four unequal quadrants in one or more of which a cell is seen to have cut off segments. These observations correspond with Bower's findings in *O. reticulatum* (1896). Apparently my material is too young to show the origin of the sporangiogenic bands, for none of the cells differ from the rest in density of the protoplasm. The next stage represented in the Florida material (fig. 18) shows the sporogenous tissue segregated into two rows of well-defined nearly spherical groups having a diameter of about 0.2 mm., and sunken below the surface of the spike by about four layers of wall cells. In these groups the cells are much less vacuolate than are the wall cells, and hence stand out clearly. At this stage none of the cells can be identified as tapetal. Frequent mitoses are found in the sporogenous groups, which grow until they reach a diameter of at least 0.25 mm. without further differentiation. During this stage at least four successive divisions of the sporogenous cells probably occur, resulting in the formation of groups of sporocytes. During the growth period the cells vary in shape but are mostly rectangular rather than polygonal, are fitted tightly together, and are separated by thin but clear walls. The nuclei measure about 20 µ in diameter, except in scattered cells in which divisions fail to occur and the nuclei may be over 30 µ wide. As the divisions proceed, the walls begin to separate, a process which cannot be attributed altogether to shrinkage during preparation of the material, because at this stage there is a marked increase in the dimensions of a sporangium, leading to production of a cavity which becomes occupied by tapetal plasmodium as well as developing spores. The dividing sporogenous cells adhere to each other in the so-called blocks, which are said to be characteristic rather of *Botrychium*, but are sometimes rather pronounced in *O. palmatum* (fig. 13). It is noticeable that cell-division is not simultaneous in different blocks, hence the spotty appearance of a developing sporangium. In some of the blocks eight regularly arrranged sporocytes may be seen, with indications of a second layer beneath the group of eight seen in the plane of the section. Before the blocks entirely break up some of the sporocytes have passed into the leptonema stage of meiosis, so that their nuclei present an entirely different appearance from that of the adjoining tapetal nuclei or of the other stages in development of sporogenous cells. Certain nuclei show a stage much resembling a "leptotène bouquet"; it is regarded as possible that these may be the result of imperfect fixation. As the sporocytes become separated and float in the plasmodium, pairing of chromosomes can be made out, and older cells have their nuclei plainly in diakinesis (fig. 14); here the chromosomes, usually slender as well as small, have become exceedingly short and stubby, and can be interpreted as tetrads. In other sporocytes (fig. 19) the chromosomes are seen to be disposed upon the equatorial plate, and a polar view brings out the large number, estimated in other species to be over 100 (Burlingame 1907; Maheshwari and Singh 1934). Division II follows promptly upon completion of the first, and appears to be uniformly so inclined as to give rise to a quartet of tetrahedral spores. Cytokinesis is deferred until after division II. Certain apparent differences in size of the chromosomes are probably to be interpreted as due to overlaps; the small size of the chromosomes lends support to such a view. The mature spores retain the triradiate marking and have a finely papillate surface. Their diameter is 0.05 mm. and the wall is 3 µ in thickness.

Tapetum. The determination of the origin of this layer presents difficulties. When first distinguishable it consists of somewhat flattened rather deeply staining cells, more or less clearly in the same radial rows as sporogenous cells; mitoses however have not been observed. In later stages the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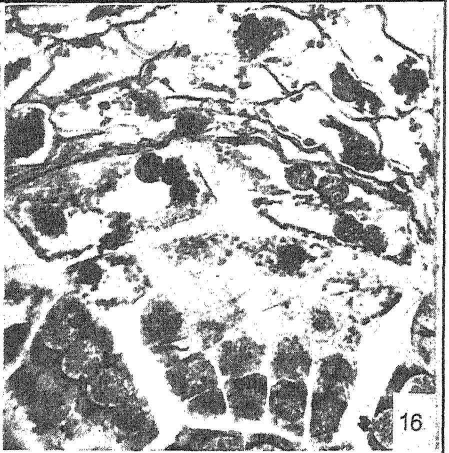
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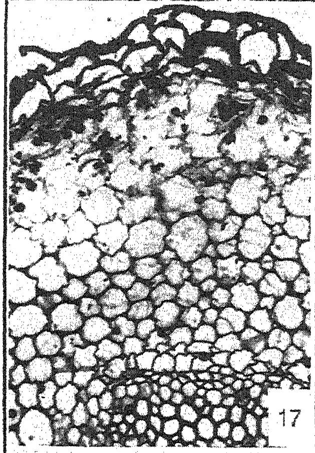
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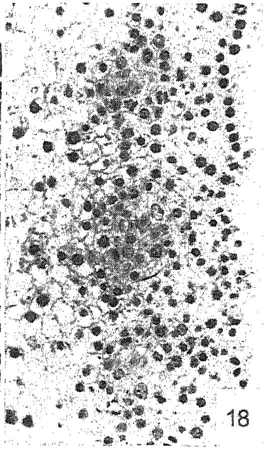
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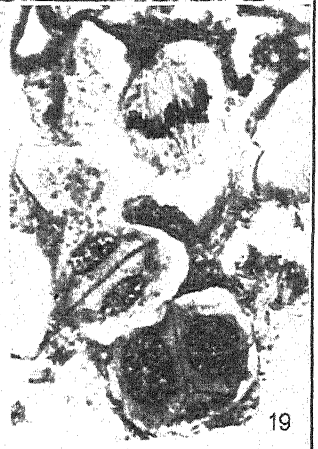
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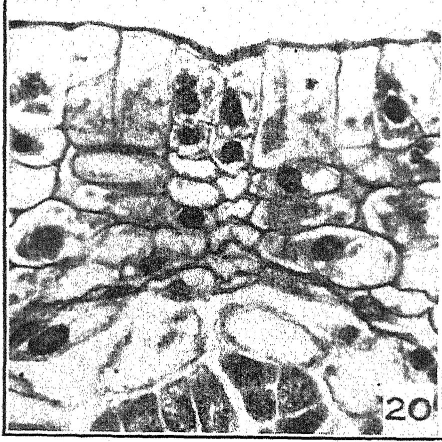
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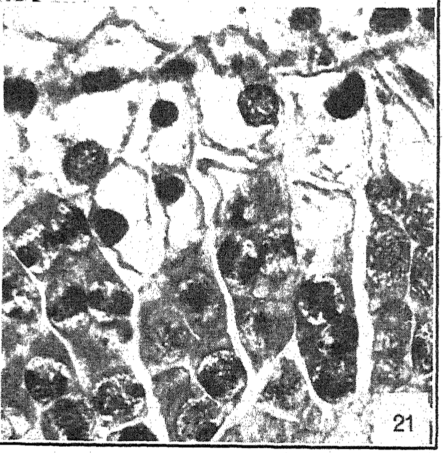
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tapetal cells have increased in radial diameter and are distinctly more vacuolate than the sporogenous cells. It can then be seen that in certain cases the outer edge of the sporogenous mass of cells is uneven, a tapetal cell sometimes replacing a sporogenous cell (fig. 15). Again, what appear to be sister cells as evidenced by their position in radial rows are developed inwardly as sporogenous cells and outwardly as tapetum (fig. 21). This may be taken as evidence that the tapetal cells are potentially sporogenous. The thickness of the tapetum is from two to three layers. In figures 13 and 15 there is an appearance of a wall surrounding the sporangium; this is due to the collapse of inner jacket cells at the time of increase in volume of the sporangium, previously mentioned. Part of this increase is probably due to changes in shape, size, and number of the tapetal cells. These changes are going on quite actively while the sporogenous cells are giving rise to sporocytes, as is evidenced by the rather frequent mitoses visible in the tapetal layer (fig. 7). Some of the mitoses are completed, so far as the nuclei are concerned, giving rise to binucleate cells (figs. 8, 15), which are numerous if not indeed typical of this stage. Quadrinucleate cells also occur (fig. 16) but are distinctly less numerous than the binucleate ones. Some of the cells contain a single nucleus of spherical or irregular shape, measuring 30–34 μ in diameter instead of the 17–20 μ found in other tapetal cells (fig. 15). These observations indicate that in such cells the mitoses have been incomplete (fig. 11) or possibly that nuclear fusions have taken place. Figure 9 shows a particularly broad metaphase of width over 50 μ (cf. fig. 7); similar figures have been found showing the equatorial plate in face view, and these plainly indicate that the nuclei are heteroploid. No convincing appearances of amitosis have been found, but abnormal mitoses (fig. 10) sufficiently account for the diversity in size and shape of the nuclei. Steil (1935) has figured many similar cases in other members of the order, so that it is unnecessary to pursue the matter further than to refer to the frequency of such phenomena in our material.

The cells are now seen to have one or more large vacuoles, while the walls, heretofore distinct though thin, begin to melt away. In this way is produced a plasmodium which is presently seen occupying the spaces between the

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Explanation of figures 15–21

FIG. 15. Medium stage of development of sporangium, showing the apparent wall, binucleate tapetal cells, and probably sterilized cells of potential sporogenous tissue, with normal sporocytes. × 200. FIG. 16. Sporangium at about the same stage as figure 15, with a quadrinucleate tapetal cell at left, and two binucleate cells at right. × 200. FIG. 17. General view of root, showing outer cortex, fungal layer, inner cortex, and part of stele with diarch xylem. × 70. FIG. 18. Young fertile spike with sporangia not yet showing tapetum. × 200. FIG. 19. Dividing sporocytes in plasmodium. Above is a metaphase, below this a telophase and a quartet. × 600. FIG. 20. Region of spike opposite a sporangium, where dehiscence takes place. "Wall" of sporangium, tapetum and sporogenous cells are also shown. × 120. FIG. 21. Tapetal cells in radial alignment with sporogenous cells. × 200.

"blocks" of sporocytes and later separating the individual spores (fig. 12). The plasmodium shows numerous vacuoles, also nuclei of various sizes and shapes which persist after the spore quartets are formed.

Shortly before the sporocytes are formed the edges of the spike show externally a series of slight depressions, one opposite each sporangium. In section the jacket cells are seen (fig. 20) to have divided periclinally in a more or less regular manner below each of the depressions. Later a transverse split appears at each of these points, setting free the spores. No other specialization connected with dehiscence can be seen.

DISCUSSION

Campbell (1911) came to the conclusion that in the Java material identified as *O. moluccanum* Schlect. there is no true "cauline" stele, basing his opinion on the observation that the vascular tissues are made up entirely of leaf traces and do not receive additions from the apical tissue of the stem. More recently Maheshwari and Singh (1934) observe with reference to *O. fibrosum* "there is no cauline stele; it is made up entirely of leaf traces." They mention moreover the presence of the commissure which is present at each leaf gap also in *O. palmatum*. It is worthy of remark that in each of these species there is a more or less tuberous rhizome (v. Campbell 1911, fig. 55; Maheshwari and Singh 1934, fig. 45). On the other hand, in the more slender rhizome of *O. Engelmanni* Prantl, material of which has been kindly supplied by Dr. E. P. St. John, I have observed a simple siphonostele with somewhat overlapping gaps from the edges of which two leaf traces arise. It would be possible to interpret the vascular system of the rhizome of *O. palmatum* as a congeries of leaf traces, but I prefer to follow Bower (1911, p. 281) in regarding the scattered condition of the stele as "a natural consequence of the parenchymatous swelling" which characterises this species as it does the other two mentioned previously. Attention may be drawn to the overlapping of characters in the three sections of the genus, such as the double leaf trace, the commissure, the different types of stele. As to the double leaf trace, which Bower (1911) considers a character in which *Ophioderma* and *Cheiroglossa* differ from all other Ophioglossaceae, it occurs not only in *O. Engelmanni*, a representative of *Euophioglossum*, but is seen in some of my preparations of *Botrychium dissectum*. Thus is emphasized the essential unity of the order.

The origin of the tapetum appears to vary in the three genera. Bower (1908) sums up the situation thus: "the large sporogenous mass of *Ophioglossum* throws off its superficial tissues as tapetum, . . . in the other two genera the tapetum originates from the adjoining tissue" (p. 457). The observations recorded in the present paper are in agreement with Bower's statement, and add an item to the list of features in which section *Cheiroglossa* is truly an *Ophioglossum*.

The shape of the mature tapetal cells varies from flat in *Botrychium* to irregularly cubical or polygonal in *O. palmatum*, and distinctly elongated radially in *Helminthostachys*.

As to the later stages in development of the tapetum, Steil (1935) was able by the use of satisfactory material of *B. virginianum* and *O. vulgatum* not only to find binucleate cells, which were lacking in the material used by Burlingame (1907) and Maheshwari and Singh (1934), but to furnish evidence for deriving these from incomplete or abnormal mitosis rather than amitosis. It is of interest to note that the tapetum of *O. palmatum* presents many stages closely resembling those figured by Steil and thus bears witness to the unity of the order in this regard. The presence of many tapetal nuclei dividing by mitosis, observed by Steil and now confirmed in the material of *O. palmatum*, goes far to dispose of the older theory which accounted for polynucleate tapetal cells by assuming amitosis. I have seen no cases in the Florida material that could not be explained on the basis of incomplete or abnormal mitosis.

Passing to the nature of the fertile spike, which is of course the central problem in the order, it would appear unnecessary to review the older theories, for several of these have been expressly relinquished by their supporters; and yet these theories have a way of gaining a new lease of life as a result of changing points of view or of more recent discoveries, for instance the adoption by Bower (1935) of the theory proposed in 1930 by Zimmerman, to the effect that the fertile spike represents a dorsi-ventral dichotomy of some ancient pteridophytic shoot. This case is the more interesting in view of the fact that Bower has entertained at least two other hypotheses: in 1908, etc., the strobilar nature of the *Ophioglossum* plant, and in 1926 the theory proposed by Roeper in 1859 to the effect that the fertile spike in *Botrychium* represents two fused basal pinnae.

It will readily be perceived that these three theories have entirely different starting points; for instance, what we may style the "dichotomy" view presupposes an origin for Ophioglossales quite early in the history of the megaphyll, while Roeper's theory of fusion assumes that the fern leaf was already existent before Ophioglossales branched off from the ancestral stock. It is at present not possible to exclude either of these possibilities, but it is well to bear in mind that the members of Ophioglossales which best illustrate a possible antero-posterior dichotomy are species of *Botrychium* of small size, usually regarded as reduced forms. I refer particularly to certain abnormal specimens of *B. simplex* Hitchc. in which large sporangia occur in both sterile and fertile segments. These could be interpreted as representing dichotomy in two planes, but their vascular as well as photosynthetic organs bear evidence of reduction. Other phases of this question are reserved for separate treatment.

The genus *Ophioglossum*, earlier considered primitive, is now regarded as the most advanced of the three genera, on the basis of venation, vascular structure, and sporangia. Within the genus, those species having a single spike are generally regarded as typical, while *O. palmatum* is accordingly an elaborated form showing duplication or chorisis (*pleiogeny* is the word Bower, 1911, suggests for such phenomena). It is possible, however, that this plant represents a form more nearly like the ancestral stock than do the other species, while the small species with unbranched sterile segment and single spike are reduced forms. Such a view is suggested though not explicitly stated by Eames (1936), and with this view I believe the balance of evidence is in accord. First, in *O. palmatum* the repeated dichotomy shown in juvenile stages and also in many adults appears like the persistence of a very ancient habit. The spikes with their truly lateral (marginal) position may represent specialized lobes, as was suggested in earlier papers (Chrysler 1910, 1911). Second, the venation does not show the specialization found in some of the smaller species. In the latter a more or less pronounced midvein is frequently visible in specimens which have been rendered translucent. A number of preparations illustrating this feature, also unpublished results, have most generously been put at my disposal by Dr. E. P. St. John. In *O. palmatum* on the other hand no such differentiation of veins can be made out. Moreover it has already been pointed out that the network is on a simpler plan, more suggestive of derivation from dichotomy, than is the case in some species of *Euophioglossum*. Third, occasional cases of dichotomy are found in the sterile segment of small species. Fourth, a reduction series starting with *O. palmatum* duplicates the series which seems to be very probable in the genus *Botrychium*.

Against such a sequence may be urged the epiphytic habit in both of the large-leaved sections, *Ophioderma* and *Cheiroglossa*. Further, it is true that the arrangement of the fertile spikes is not very suggestive of dichotomy; much modification of the original condition is indicated, although the true marginal position of the spikes is probably significant. It seems certain, as is indicated on general grounds, that before *Botrychium* and *Ophioglossum* became separate genera the habit of fusion of the two basal lobes had already become settled.

Although the danger of introducing teratological evidence is admitted, it should be mentioned that the Florida material includes several spikes which are distinctly flattened, with a relatively broad thin lamina between the two rows of sporangia. Such cases may give us a glimpse of the appearance of the ancestral fertile lobes (fig. 4).

Another suggestion as to the possible appearance of the ancestral *Ophioglossum* comes from the remarkable genus *Trochopteris* (Bower 1926, p. 162), sometimes included under *Anemia*. In the leaf of this plant the basal lobes bear sporangia in the marginal position. Recalling the morphology of the typical *Anemia* leaf, *Trochopteris* may well represent the persistence of an ancestral condition. The "monangial sorus" in Schizaeaceae may be indication of affinity with Ophioglossales, while the pronounced dichotomy in *Schizaea* marks the family as a primitive one, to which we may reasonably turn when seeking a parallel to the evolutionary history of Ophioglossales.

The most recent proposal concerning the morphology of the Ophioglossales is by Troll (1933), who has extended to this group his view of the peltate nature of the leaf of certain higher plants. He considers that *O. palmatum* best of all members of the order illustrates the peltate structure. He finds a parallel in the genus *Rodgersia* (Saxifragaceae), which would seem to be a rather advanced group in which to seek ancestral features. Moreover Troll admits having had no new material of *Ophioglossum* for study. He hazards the opinion that the cylindrical ("unifazial") structure of the petiole is so fixed that it no doubt occurs in sterile fronds as well as those which bear an adaxial spike. Unfortunately for the theory, my material has furnished an opportunity to test out this assumption, and I am in a position to say that in sterile leaves the vascular system of the petiole forms a C but the edges fail to close in to form an O; on the contrary the C opens out widely as soon as the rod-like petiole merges into the blade. It follows that Troll's schematic figure (1933, p. 570), explaining the plan of the leaf in *O. palmatum*, simply does not hold. Further, the evidence derived from abortive spikes proves nothing. This must surely be reasoning backwards, and is contradicted by the evidence from juvenile plants.

Most likely the occurrence of the strongly curved vascular system in the petiole of this plant is to be explained in terms of the mechanical necessities of a large heavy leaf, and we may interpret the C-shaped vascular system as a mere temporary "expedient" providing the necessary rigidity. If this is the correct interpretation we may go farther and suggest that the close approximation of the two edges of the C played a part in the evolution of a *single* spike in the adaxial position. The following stages are represented in the Florida material: (1) two basal spikes, closely approximated on the adaxial face of the petiole; (2) one adaxial (median) stalk which forks giving rise to two spikes; (3) the regular single basal spike supplied by a larger number of bundles than is the case in lateral spikes. In all of these cases the insertion of the spikes is really marginal, as is indicated by the vascular connections.

This short survey of theories leaves the writer with the idea that evidence for deriving Ophioglossales directly from plants which still had a primitive megaphyll, showing dichotomy in two planes, is still too scanty to be convincing, attractive as the general proposal appears. The evidence from *O. palmatum* and from more general considerations appears to favor the proposition that the dorsiventral leaf had already appeared, but that dichotomy in one plane was still pronounced in the ancestors of the group.

SUMMARY

1. An adequate supply of suitably preserved material of *Ophioglossum palmatum* L. from Florida has made it possible to fill the chief gaps in our knowledge of the sporophyte.
2. The mycorrhizal condition is restricted to the root, where its occurrence is local.
3. The apical cell of the root has the usual tetrahedral form, with four cutting faces.
4. The development of spores and tapetum is traced. In the latter numerous binucleate cells and abnormal mitoses are found.
5. The lobing of the leaf is essentially dichotomous, as is seen in juvenile stages and in many mature individuals.
6. Venation is of a less advanced reticulate type than is shown in some species belonging to *Euophioglossum.*
7. The observations of Bower concerning the vascular plan of rhizome and petiole are confirmed.
8. It is held that the insertion of the fertile spikes is truly marginal. The lowest spike usually represents the fusion of two.
9. Evidence is adduced for the view that *O. palmatum* is nearer the ancestral condition than are the smaller species.
10. The overlapping of various features which have been used to distinguish the three subgenera of *Ophioglossum* indicates the essential unity of the genus.
11. Certain current theories as to the nature of the fertile spike are criticized in the light of recent observations.

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THE GENUS EVERARDIA

CHARLES GILLY

(WITH THREE FIGURES)

INTRODUCTION

During 1939, when identifying the specimens of Cyperaceae which Mr. G. H. H. Tate collected on Mount Auyan-tepui (5), I had occasion to examine the specimens which he brought back from earlier expeditions to Mount Roraima and Mount Duida. These included several unnamed specimens (numbers *469, 542, 720, 721, 800,* and *816*) provisionally referred to the genus *Everardia* by Britton (4).

It must be presumed, for several reasons, that Britton made only a casual inspection of these specimens. In the first place, I must disagree with his observation that these unnamed specimens are "not in good condition"; certainly complete vegetative portions of the plants, together with mature achenes and well-preserved anthers on almost every specimen, constitute excellent condition, especially in the Cyperaceae. Secondly, certain of these specimens were so different from the rest, and from the two known species in this genus, that the possibility of including them in *Everardia* seemed slight. Subsequent study showed that *Tate 720, 721,* and *800* must be referred to the genus *Cephalocarpus* Nees. *Tate 542* is neither an *Everardia* nor a *Cephalocarpus*, although it does possess some characters of both genera; neither can it be placed in the rather closely related genus *Lagenocarpus* Nees. Probably this staminate specimen represents the only collection of an as yet undescribed genus.

Tate 426, from Mount Roraima, identified tentatively by Britton as *Everardia angusta* N. E. Br., is distinct from that species. *Tate 638,* also from Roraima, proves to be distinct from *E. montana* Ridley. *Tate 570,* provisionally referred to *Lagenocarpus rigidus* Nees in the Duida report (4), cannot be included in the genus *Lagenocarpus* but represents an undescribed species of *Everardia. Tate 469* and *816,* already mentioned, are conspecific and represent another undescribed species. These four new species, described in the present paper, together with *E. longifolia* from Mount Auyan-tepui (5), increase the number of species in this genus from two to seven.

In regard to the publication date of the genus *Everardia,* I quote a self-explanatory paragraph, signed by the Secretary of the Linnean Society of London, which precedes Oliver's paper on the im Thurn collections from Mt. Roraima (8): "Note.—The following determinations and descriptions of new plants were expressly drawn up for publication in the 'Transactions of the Linnean Society,' a confidential copy being given to Mr. E. F. im

Thurn to help him in writing the foregoing Introduction. During the delay required to prepare the accompanying Plates, Mr. im Thurn has taken the unprecedented course of printing the whole of the unrevised draft, at Demarara, in 'Timehri, the Journal of the Royal Agricultural and Commercial Society of British Guiana,' vol. v. pp. 145–233 (Dec. 1886), thus forestalling the present publication.—Sec. L. S.'' Because of Mr. im Thurn's ''unprecedented course,'' it seems necessary to cite the publication of the genus *Everardia* Ridley as ''in im Thurn, Timehri **5**: 210. Dec. 1886'' (7), despite the fact that in the Index Kewensis the Timehri citation is relegated to brackets and preference given to ''in Oliver, Trans. Linn. Soc. *Ser. II,* **2**: 287. July, 1887.'' The same consideration must also apply to the publication and citation of the species *E. montana* Ridley.

I quote from Ridley's generic description: ''Stylus brevis, stigma *bifidum* lobis brevibus planis lanceolatis.'' And from his description of the species *E. montana:* ''Stigma breviter *bifidum* lobis lanceolatis obtusis planis, violaceis.'' And, again, from his next succeeding paragraph: ''This genus is most nearly allied to *Lagenocarpus,* but differs entirely from that genus, and from the rest of the Cryptangiae, in the lateral inflorescence, the *bifid* stigma, with short flat lobes, the absence of any cupule, and the presence of a large number of hypogynous bristles.'' (Except for the generic name, the italics in the preceding quotations are mine.) I do not know whether Ridley was merely careless in his diagnosis, or whether he happened to choose, for his examination, pistillate flowers from which one of the stigmas had been broken. It is sufficient to say that the remaining pistillate flowers on the type specimen distinctly show *three* stigmas, and the artist who made the drawings for plate 52 (8) portrayed *three* distinct stigmas in both of his delineations of the pistillate flower. I cannot agree, however, with either Ridley's description or the artist's portrayal of the shape of the stigmas. Ridley's comments are quoted above; the artist has shown the stigmas as little more than twice as long as wide, and as distinctly flattened-lanceolate in shape. My examination of the pistillate flowers of the four available specimens (the type included) of *E. montana* shows the stigmas to be linear, elongated and approximately terete, with, in some flowers, a very slight tendency toward inflation at the point of their separation from the style proper. The stigmas of the other six species of the genus are elongate and terete.

Examination of the achenes of the seven known species of this genus discloses that the ''Setae hypogynae, copiosae, tortae'' of Ridley (7), and the ''pili hypogyni copiosi'' of Brown (1), must be more fully explained. Even low magnification (×10) shows that the achenes of *Everardia* are seated in a hypogynous perianth cup formed by the marginal fusion of three minute scales, the free upper portions of which appear to be ciliate-margined. Higher magnification (× 100) shows that these scales are formed of a single layer of unicellular hairs. The basal portions of these hairs are fused, thus forming the "scales," but above the area of fusion the individual hairs are free. The structure of these perianth scales is similar to those of the African genus *Microdracoides* Hua (2, 6) which may ultimately prove to be closely related to *Everardia.*

The arrangement of the inflorescence, as described by both Ridley and Brown, with staminate spikelets below and pistillate spikelets above, is borne out by the additional five species. The spikelets of the two sexes, however, are not wholly segregated. Occasional pistillate spikelets may be found at the apices of lower compound branchlets, or at the apex of the central branchlet arising from one or more of the lower inflorescence sheaths. Also, but not so frequently, occasional staminate spikelets are found on branchlets arising from the uppermost inflorescence sheaths.

The true stem (which in most Cyperaceae is very short) elongates from year to year. This stem should perhaps be termed an aerial rhizome, for, as it elongates by growth (the plant thus gradually becoming more and more top-heavy), "prop roots" are formed along its length. These "prop roots" force their way through the persistent leaf-sheaths which surround the stem and, after reaching the ground, aid in supporting the top-heavy plant. There seems to be no regular pattern, such as is exhibited by the axillary buds, for the formation of these "prop roots."

In his description of *E. angusta,* Brown (1) makes the statement: "Leaves in dense tufts of 3–6, distinct from the flowering culms . . ." An examination of the three available specimens (the type included) of *E. angusta* and of *Tate 426* from Mount Roraima explains this observation (by Brown). I have found that in this genus the leaves (as is typical of the entire family) are distinctly three-ranked, and that, at the point of attachment of the bases of their closed sheaths to the aerial rhizome, a distinct scar which encircles the rhizome in a closed band is formed. Between each scar and the next above—in the axil, therefore, of each leaf—is an axillary bud which sometimes remains dormant, sometimes produces an inflorescence, and sometimes develops into a branch of the rhizome. It was, undoubtedly, these young and few-leaved rhizome branches which Brown observed. Further to add to the illusion of distinct flowering culms and fascicled leaves, the flowering culm of the year seems always to be developed from the bud in the axil of about the sixth leaf below the growing tip of the rhizome.

For suggestions and advice on this problem, I wish to thank Dr. H. A. Gleason; and for his kindness in lending me the types and other available specimens of *E. angusta* and *E. montana,* I express my thanks to Sir Arthur W. Hill, Director of the Royal Botanic Gardens at Kew.

TAXONOMIC TREATMENT

Because of the discrepancies or omissions which I have already mentioned, and because of certain other points which have been observed in the study of the additional species, it seems necessary to emend the genus *Everardia* Ridley as follows:

EVERARDIA Ridley, in im Thurn, Timehri 5: 210, 1886. Perennial, with an ascending, simple or branched, woody aerial rhizome surrounded by the persistent and more or less ragged sheath-bases of old leaves. Leaves rigid, more or less carinate, three-ranked, but sometimes appearing many-ranked. Flowering culms erect, leafless, axillary, basally enclosed by a short membranous sheath which is usually hidden within the leaf-sheath. Inflorescence composed of few–numerous tufts of erect, simple, or compound branchlets arising from the axils of close-fitting leafy-pointed sheaths. Spikelets monoecious, solitary at the apices of the branchlets. Lower portion of the inflorescence staminate or with 1–several pistillate spikelets at the apices of the compound branchlets or the central branchlet of a tuft or tufts bearing a solitary pistillate spikelet. Upper portion of the inflorescence wholly pistillate or rarely with 1–few staminate spikelets accompanying the pistillate. Staminate spikelets numerous, many-flowered; empty glumes 3–8, staminiferous 4–8; stamens under each staminiferous glume 6 (or rarely 4 or 8). Filaments capillary, persistent; anthers linear, two-celled, the connective prolonged between the loculi into a minute tuft of stiff hairs. Pistillate spikelets few and smaller than the staminate, 1-flowered, the ovary surrounded by 4–6 glumes. Achene from terete to obtusely-triangular, more or less conspicuously marked by 3 longitudinal carpellary lines, the apex tapering into a persistent, pubescent, or glabrous, conical, acute or truncated beak (style base), the body of the achene glabrous or pubescent. Style exserted, the stigmas 3, essentially terete, linear, elongated; style and stigmas conspicuously pubescent. Perianth cupular, formed by marginal fusion of 3 minute ciliate-margined scales, the scales frequently so reduced in size that the achene appears to be surrounded by a ring of hypogynous hairs; marginal hairs straight or twisted.

TYPE SPECIES: *E. montana* Ridley.

The genus *Everardia* belongs to the tribe Cryptangiae, the most closely related genera being *Cephalocarpus* and *Lagenocarpus*. Both *Everardia* and *Cephalocarpus* have axillary flowering culms and the perianth cup of three fused hypogynous scales; they may thus be distinguished readily from *Lagenocarpus* with its terminal inflorescence and lack of perianth. *Everardia* is easily separable from *Cephalocarpus*, the latter genus having capitate-condensed inflorescences and achenes with clavate, persistent beaks. *Everardia* has 6 stamens under each staminiferous glume of the staminate spikelets; both *Cephalocarpus* and *Lagenocarpus* have 2 stamens under each staminiferous glume.

Although Ridley published no formal dedication of the genus, the fact is obvious that *Everardia* is named in honor of Everard Ferdinand im Thurn (1852–1932), collector of the generic type specimen.

So far as is now known, the genus *Everardia* is restricted to the summits of Mount Roraima, Mount Duida and Mount Auyan-tepui, but future exploration will undoubtedly discover the present known species and/or other species on other mountains in the Sierra Pacaraima complex. The accompanying map (fig. 1) shows the type localities of the species in this genus. It is of interest to note that, thus far, not one of the seven species has been collected from more than a single mountain.

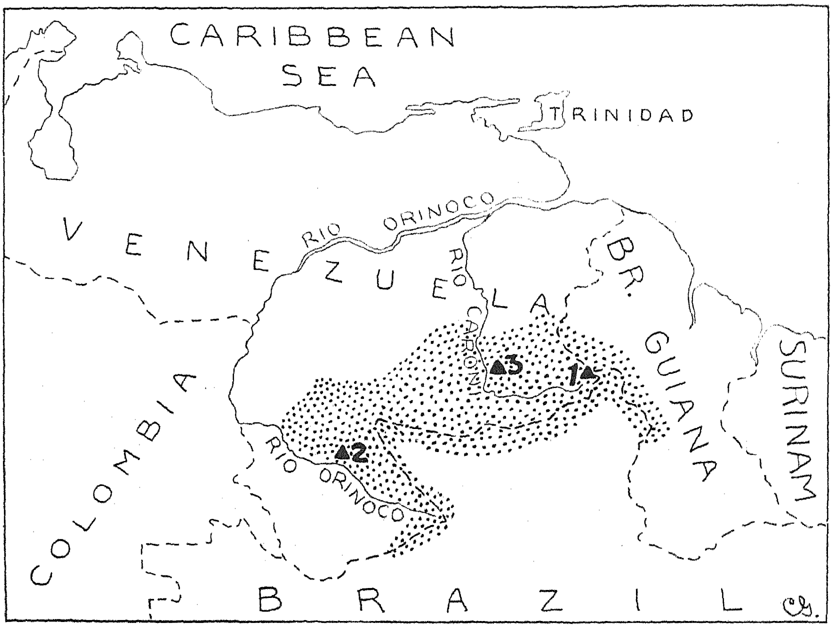

FIG. 1. Distribution of *Everardia*. 1. Mt. Roraima (*E. angusta*, *E. gracilis*, *E. montana*); 2. Mt. Duida (*E. glaucifolia*, *E. revoluta*, *E. duidae*); 3. Mt. Auyan-tepui (*E. longifolia*). General outline of the Sierra Pacaraima complex indicated by dotted area.

The specimens which I have examined in the study of this genus are deposited in the herbarium of the New York Botanical Garden (NY), and in the herbarium of the Royal Botanic Gardens at Kew (K).

KEY TO THE SPECIES

Leaves 4 mm. or less in width, folded for most of their length, thus appearing triangular in cross-section, thinly pilose on both surfaces and margins; beak of achene conical, longer than body of achene, densely stiff-pubescent.

  Achene dark brown, both body and beak pubescent; perianth scales obovate; leaves 2–3.5 dm. long; flowering culm, inflorescence included, 3.5–5 dm. high. 1. *E. angusta*

  Achene straw colored, the body glabrous and beak pubescent; perianth scales acute-triangular; leaves 0.7–1.5 dm. long; flowering culm, inflorescence included, 2–3 dm. high .... 2. *E. gracilis*

Leaves more than 4 mm. in width, flattened, folded or with revolute margins (when folded, not appearing triangular in cross-section), the margins various but the leaf-surfaces not pilose; beak of achene conical or truncated-conic, if longer than the body of the achene, then the beak glabrous or only minutely puberulent.

Flowering culm and inflorescence stiffly erect, considerably exceeding the leaves; leaves stiffly erect, the margins parallel for most of their length.

Leaves 4–6 mm. wide, 1.5–4 dm. long, thin, green, glabrous, with prominent midrib; staminate spikelets 7–11 mm. long, sterile glumes brown, oblong, bifid at apices, the green midrib extended between the teeth into a mucro 1.5–2.5 mm. long .... 3. *E. longifolia*

Leaves 12–14 mm. wide, about 5 dm. long, thick, leathery, white-glaucous on both surfaces, the midrib obscure or almost obsolete; staminate spikelets 3.5–4 mm. long; sterile glumes purple-brown, broadly ovate to ovate-lanceolate, short mucronate but not bifid at apices .... 4. *E. glaucifolia*

Flowering culm and inflorescence laxly ascending or more or less erect, scarcely exceeding the leaves; leaves reflexed or recurved, broadest at base and gradually tapering toward apices.

Leaves conspicuously revolute, appearing hollow-terete in cross-section, the margins smooth; achene light brown, the tricarpellary markings distinct; beak of achene slender, conical, half as long as body of achene. .... 5. *E. revoluta*

Leaves folded or flattened, the margins ciliate or sharp-scabrous; achene dark brown, the tricarpellary markings faint; beak of achene conical and as long as achene body or bluntly truncated-conic and equalling or shorter than achene body.

Sheaths of inflorescence glabrous except for scanty pubescence at their mouths; beak of achene conical; leaves 10–15 mm. wide at base, folded at base, smooth and glabrous except for the white-ciliate margins; flowering culms stout, flattened .... 6. *E. montana*

Sheaths of inflorescence densely minute-pubescent; beak of achene bluntly truncated-conic; leaves 5–8 mm. wide at base, flat for entire length, upper surface granular-roughened, the lower smooth and glabrous, the margins sharp scabrous; flowering culms capillary, subterete .... 7. *E. duidae*

1. EVERARDIA ANGUSTA N. E. Brown, Trans. Linn. Soc. II, **6**: 73. 1901. *Cryptangium stamineum* N. E. Brown; Clarke, Kew Bull. Add. Ser. **8**: 135, nomen. 1908.[1]

Aerial rhizome simple or branched, 2–3 mm. in diam., to at least 5 cm. long, surrounded by the ragged, fibrous, dark brown leaf-sheaths. Leaves 2–3.5 dm. long, 2–4 mm. wide, linear, acute, usually folded below, bicarinate above, appearing triangular in cross-section, more or less recurved, thinly pilose. Flowering culms strictly erect, flattened, slightly concave on one side, convex on the other, sparingly pilose to glabrate, about 1.5 mm. wide, including the inflorescence 3.5–5 dm. high; basal sheath 5–7 cm. long. Inflorescence 3.5–5 dm. high; basal sheath 5–7 cm. long. Inflorescence of 4–5 distant tufts of spikelets; sheaths dark brown, glabrous or thinly pilose, 8–20 mm. long, the leaf-like points about one-third longer than the sheaths. Staminate spikelets 7–8 mm. long, 2–2.5 mm. in diam.; sterile glumes 5–7, oblong, acute, mucronate, brown, thinly and minutely pubescent on the back; staminiferous glumes 4–6, oblong, obtuse; stamens under each glume 6. Pistillate spikelets 6 mm. long, 1.5 mm. in diam.; glumes 5, oblong-lanceolate, acute, mucronate, minutely ciliate. Achene subterete, ovoid, pubescent, dark brown, 2–2.5 mm. long, about 1 mm. in diam., the tricarpellary markings distinct; beak persistent, long-conic, about 3 mm. long, densely covered with short, dark brown pubescence. Perianth scales obovate, about one-eighth as long as body of achene; marginal hairs copious, about half as long as body of achene. Stigmas linear, terete, dark brown. (Fig. 2, *a*, *a′*.)

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[1] Pfeiffer (9, p. 44) states that the nomen nudum *Cryptangium stramineum* [sic!] N. E. Br., refers to this species. In my examination of the type specimen, I find the crossed-out name *Cryptangium*, in Brown's handwriting, above the name *Everardia angusta*. Following this is an erasure through which may be dimly seen "*stamineum.*" It is indeed unfortunate that this cheironym was inadvertently published in Clarke's posthumous Cyperaceae paper.

For the sake of easier comparison between species, I have, above, amplified Brown's specific description. Also, I have changed his measurements into the metric system.

VENEZUELA—BOLIVAR: Mount Roraima, summit, autumn 1898, *McConnell & Quelch 676* (TYPE) (K); 2500 m., Jan., 1910, *E. Ule 8539* (K); summit, Nov. 26, 1927, *G. H. H. Tate 435* (NY).

2. **Everardia gracilis** Gilly, sp. nov. Rhizomata breviora, ramosa, 2 mm. diam. minusve, vaginis persistentibus atro-brunneis lacerato-fibratis tecta; folia 0.7–1.5 dm. longa, 2–4 mm. lata, linearia acuta bicarinata pilosa; culmi floriferi cum inflorescentia 2–3 dm. alti; vagina ad basim 2–3 cm. longa; spiculae masculae 6.5 mm. longae, 1.5–2 mm. diam.; spiculae foemineae 5 mm. longae, 1.5 mm. diam., glumae 5; achaenia subteretia ovoidea glabra straminea, 2.5–3 mm. longa, 1 mm. diam.; rostro pubescente, 3.5 mm. longo; squamellae hypogynae triangulares quam corpus achaenii 6-plo breviores; stigmata linearia teretia pallido-brunnea.

Aerial rhizome short, 2 mm. or less in diam., branched, surrounded and hidden by the persistent, ragged-fibrous, dark-brown leaf-sheaths. Leaves 0.7–1.5 dm. long, 2–4 mm. wide, linear, acute, folded below, strongly bicarinate above, appearing triangular in cross-section, more or less recurved, thinly pilose on margins and midrib. Flowering culms stiffly erect, subterete, sparingly pilose to glabrate, 1–1.5 mm. in diam., including the inflorescence 2–3 dm. high; basal sheath 2–3 cm. long. Inflorescence of 5 tufts of spikelets; sheaths dark brown, densely appressed-pubescent to glabrous, 5–18 mm. long, the leaf-like point as long as the sheath. Staminate spikelets 6.5 mm. long, 1.5–2 mm. in diam.; sterile glumes 4, oblanceolate, acute and mucronate, brown, thinly pubescent or glabrous; staminiferous glumes 4, oblong, rounded at apex; stamens under each glume 6. Pistillate spikelets 5 mm. long, 1.5 mm. in diam.; glumes 5, narrowly lanceolate, acute, minutely ciliate on the margins. Achenes sub-terete, ovoid, glabrous, straw-colored, shining, 2.5–3 mm. long, 1 mm. in diam., tipped by persistent beak about 3.5 mm. long, tricarpellary markings distinct; beak densely covered with crisp, golden-brown pubescence. Perianth scales equilaterally triangular, one-sixth as long as body of achene; marginal hairs rather scanty, about half as long as body of achene. Stigmas linear, terete, light brown. (Fig. 2, *b*, *b′*.)

VENEZUELA—BOLIVAR: Mt. Roraima, summit, Nov. 26, 1927, *G. H. H. Tate 426* (TYPE) (NY).

3. EVERARDIA LONGIFOLIA Gilly, in Gleason & Killip, Brittonia 3: 153. 1939. Aerial rhizome simple, about 4 mm. in diam., surrounded by the persistent, dark brown, fibrous-reticulated leaf-sheaths. Leaves 1.5–4 dm. long, 4–6 mm. wide, stiffly erect, thin, green, glabrous, flattened for most of their

length, not folded below, the upper one-third or less bicarinate, margins and midrib minutely scabrous. Flowering culms stiffly erect, somewhat flattened, two-edged but not winged, slightly scabrous on the edges, 2–4 mm. wide, including the inflorescence 3.5–8 dm. high; basal sheath 2–3.5 cm. long. Inflorescence of 5 or more distant tufts of spikelets; sheaths brown, strongly-veined, glabrous, distinctly flattened and two-edged, 10–15 mm. long, the leaf-like points twice the length of the sheaths. Staminate spikelets 7–11 mm. long, 1.5–2.5 mm. in diam.; sterile glumes 5–7, brownish, oblong, obscurely 2-toothed at the apex, the green midrib extended between the teeth into a mucro 1.5–2.5 mm. long, glabrous except for sparse short-pubescence on upper margins and mucro; staminiferous glumes 4–5, lanceolate, acute to mucronate; stamens under each glume 6. Pistillate spikelets, which would be in the upper part of the inflorescence, not present owing to the condition of the specimens. Achene, therefore, unknown. (Fig. 2, *c*.)

VENEZUELA—BOLIVAR: Mt. Auyan-tepui, 2200 m., Dec. 1937, *G. H. H. Tate 1347* (TYPE) (NY).

4. **Everardia glaucifolia** Gilly, sp. nov. Rhizomata breviora, simplicia, 4–6 mm. diam., vaginis persistentibus nigro-brunneis fibro-laceratis tecta; folia ad 5 dm. longa, 12–14 mm. lata, crassa coriacea albo-glaucescentia erecta, margine superiore revoluto; culmi floriferi cum inflorescentia erecti, 7.5–9.5 dm. alti; vagina ad basim 2–3 cm. longa; spiculae masculae 3.5–4 mm. longae, 1.5 mm. diam., glumis vacuis 6–7, ovatis vel ovato-lanceolatis, ad apicem breviter mucronatis nec bifidis, glabris, glumis fertilibus 4–5, ovatis vel late lanceolatis acutis vel sub-truncatis; spiculae foemineae 2.5–3.5 mm. longae, 1–1.5 mm. diam., glumis 5–7; achaenia subteretia ovoidea glabra atro-brunnea, 2.5 mm. longa, 1.5 mm. diam.; rostro glabro truncato, corpus achaenii subaequante; squamellae hypogynae subrotundae, quam corpus achaenii 10-plo breviores, pilis quam lamina duplo longioribus tortis; stigmata atro-brunnea minute pubescentia.

Aerial rhizome very short, simple, 4–6 mm. in diam., surrounded by the persistent black-brown fibrous-ragged leaf-sheaths. Leaves about 5 dm. long, 12–14 mm. wide, thick, leathery, white-glaucous on both surfaces, stiffly erect, folded below, margins strongly revolute above, margins and mid-rib smooth, glabrous. Flowering culms stiffly erect, flattened, two-edged but not winged, glabrous or slightly roughened on the edges, including the inflorescence 7.5–9.5 dm. high; basal sheath 2–3 cm. long. Inflorescence of 7–10 distant tufts of spikelets; sheaths of the inflorescence terete, minutely appressed-pubescent on the prominent veins, brown or purple, 5–20 mm. long, the leaf-like points as long as the sheaths. Staminate spikelets 3.5–4 mm. long, 1.5 mm. in diam., numerous; sterile glumes 6–7, purple-brown, broadly ovate to ovate-lanceolate, short mucronate, not bifid at the apex, glabrous or nearly so; staminiferous glumes 4–5, ovate to broadly lanceolate, acute or sub-truncate, brownish with narrow, erose hyaline margins; stamens under each glume 6. Pistillate spikelets 2.5–3.5 mm. long, 1–1.5 mm. in diam.; glumes 5–7, broadly ovate-lanceolate, short mucronate, brown-purple with narrow erose hyaline margins. Achene subterete, ovoid, glabrous, dark brown, about 2.5 mm. long, 1 mm. in diam., tipped by a persistent, glabrous, truncated beak about as long as the body of the achene, the tricarpellary markings scarcely distinct. Perianth scales subrotund, one-tenth as long as the body of the achene, marginal hairs about twice as long as the scales, copious, twisted. Stigmas capillary, terete, dark brown, minutely pubescent. (Fig. 2, *d*, *d'*.)

VENEZUELA—TERRITORIO AMAZONAS: Mt. Duida, ridge northwest of Vegas Brook, 4400 ft., Jan. 1–4, 1929, *G. H. H. Tate 570* (TYPE) (NY).

5. **Everardia revoluta** Gilly, sp. nov. Rhizomata simplicia, 5 mm. diam., ad 10 cm. alta, vaginis persistentibus confertis atro-purpureo-brunneis rigidis coriaceis nec laceratis tecta; folia 1.5–3 dm. longa, ad 6–8 mm. lata

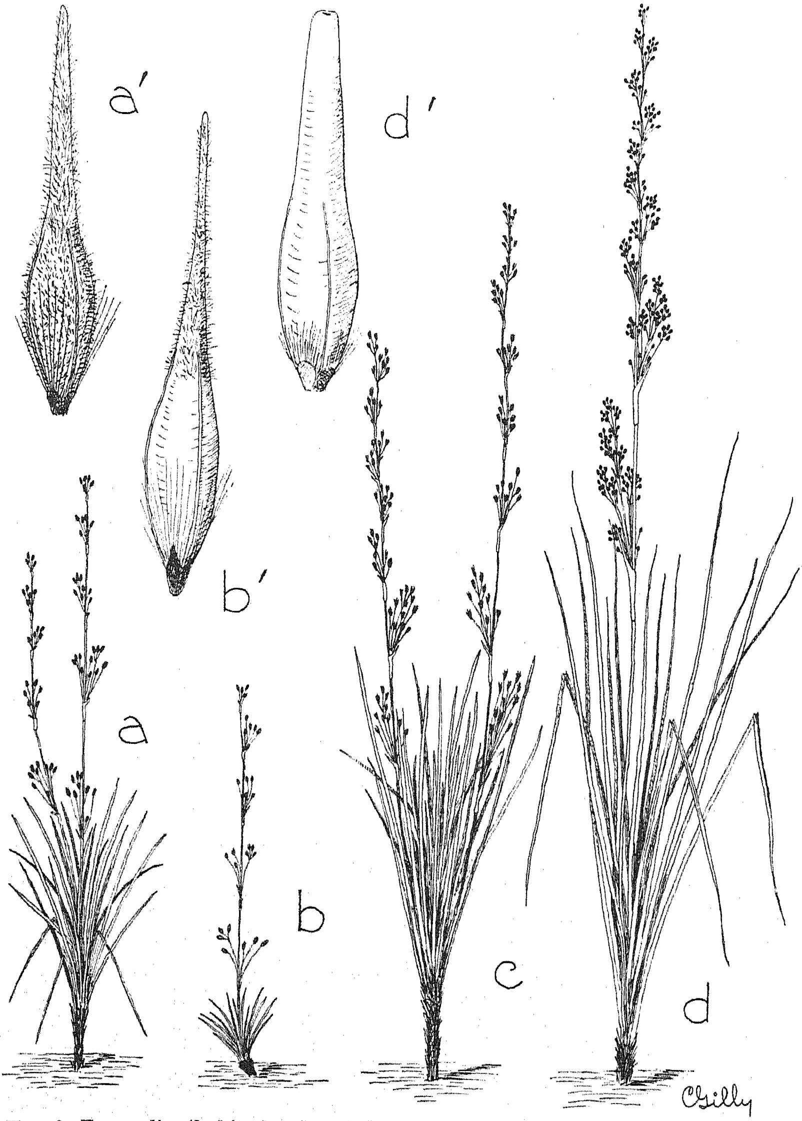

FIG. 2. *Everardia* (habit sketches ⅛ natural size; achenes × 10). *E. angustata* N. E. Br.; *a*, habit, *a′*, achene (drawn from *Tate 435*). *E. gracilis* Gilly; *b*, habit, *b′*, achene (drawn from *Tate 426*). *E. longifolia* Gilly; *c*, habit, (drawn from *Tate 1347*). *E. glaucifolia* Gilly; *d*, habit, *d′*, achene (drawn from *Tate 570*).

ad basim, coriacea glabra, margine glabro inferne complanato supra medium valde revoluta; culmi floriferi laxe adscendentes vel erecti, cum inflorescentia 2–3.5 dm. alti; vagina ad basim 1 cm. longa; spiculae masculae 4–5 mm. longae, 1 mm. diam.; spiculae foemineae 3–3.5 mm. longae, 1 mm. diam., glumis 5, lanceolatis mucronatis glabris; achaenia teretia glabra pallide brunnea, 2–3 mm. longa, 0.6–1 mm. diam., rostro gracili glabro, quam corpus achaenii dimidio breviori; squamellae hypogynae minutae orbiculares, pilis copiosis tortis ciliatis; stigmata pallide brunnea.

Aerial rhizome simple, 5 mm. in diam., to at least 10 cm. high, surrounded by persistent, crowded, dark purple-brown, firm and coriaceous leaf-sheaths. Leaves 1.5–3 dm. long, about 6–8 mm. wide at the base, gradually tapering to the apex, leathery, flattened below, entirely glabrous, the margins smooth, entire, strongly revolute above the middle, the leaf appearing hollow-terete in cross-section. Flowering culms laxly ascending to erect, flattened, two-edged but not winged, 1.5–2 mm. wide, glabrous, including the inflorescence 2–3.5 dm. high; basal sheath about 1 cm. long, entirely hidden by the leaf-sheaths. Inflorescence of 5–8 tufts of spikelets; sheaths brown, glabrous, 5–20 mm. long, the leaf-like points slightly shorter than the sheaths. Staminate spikelets 4–5 mm. long, 1 mm. in diam., sterile glumes 4, lanceolate, mucronate, glabrous, light brown; staminiferous glumes 4–6, oblong, from acute to obtuse, margins minutely ciliate; stamens under each glume 6. Pistillate spikelets 3–3.5 mm. long, 1 mm. in diam.; glumes 5, lanceolate, mucronate, the midribs prominent, glabrous. Achenes terete, glabrous, light brown, tapering to both ends, 2–3 mm. long, 0.7–1 mm. in diam., tipped by the slender glabrous beak half as long as the body of the achene, the tricarpellary markings distinct. Perianth scales, minute, orbicular, the marginal hairs two-thirds as long as the body of the achene, copious, twisted. Stigmas linear, terete, long-exserted, light brown. (Fig. 3, *e*, *e'*.)

VENEZUELA—TERRITORIO AMAZONAS: Mount Duida, crest of ridge 25, 6300 ft., Nov. 26—Dec. 16, 1929, *G. H. H. Tate 469* (TYPE) (NY); Gorge of the Cano Negro, Savanna Hills, 4000 ft., 1928–1929, *G. H. H. Tate 816* (NY).

In addition to emending the generic description, and for much the same reasons, it has seemed necessary to emend the following species:

6. **EVERARDIA MONTANA** Ridley, in im Thurn, Timehri **5**: 210. 1886. Aerial rhizome simple, about 1 cm. in diam., surrounded by the persistent, dark brown, reticulate-fibrous leaf-sheaths. Leaves 1.5–1.8 dm. long, 10–15 mm. wide at base, tapering gradually to the apex, folded below, margins slightly revolute above, leathery, glabrous except for the shortly white-ciliate margins. Flowering culms laxly ascending or sub-erect, flattened, more or less concave on one side, slightly winged, the wings minutely ciliate, 2–3 mm. wide, including the inflorescence 2–2.5 dm. high; basal sheath 3–3.5 cm. long. Inflorescence of 7–8 tufts of spikelets; sheaths of the inflorescence dark brown, somewhat compressed, from minutely pubescent to glabrate, 5–20 mm. long, the leaf-like points slightly shorter than the sheaths. Staminate spikelets 5–7 mm. long, about 2 mm. in diam.; sterile glumes 3–4, brown, strongly veined, ovate-lanceolate, glabrous, short-mucronate, sometimes minutely bifid at the apices; staminiferous glumes 5–7, lanceolate, acute or truncate, sometimes minutely mucronulate, the margins minutely ciliate; stamens under each glume 6. Pistillate spikelets 4–5 mm. long, 1–1.5 mm. in diam.; glumes 5–6, lanceolate, purple-brown, from acute to more or less mucronate.

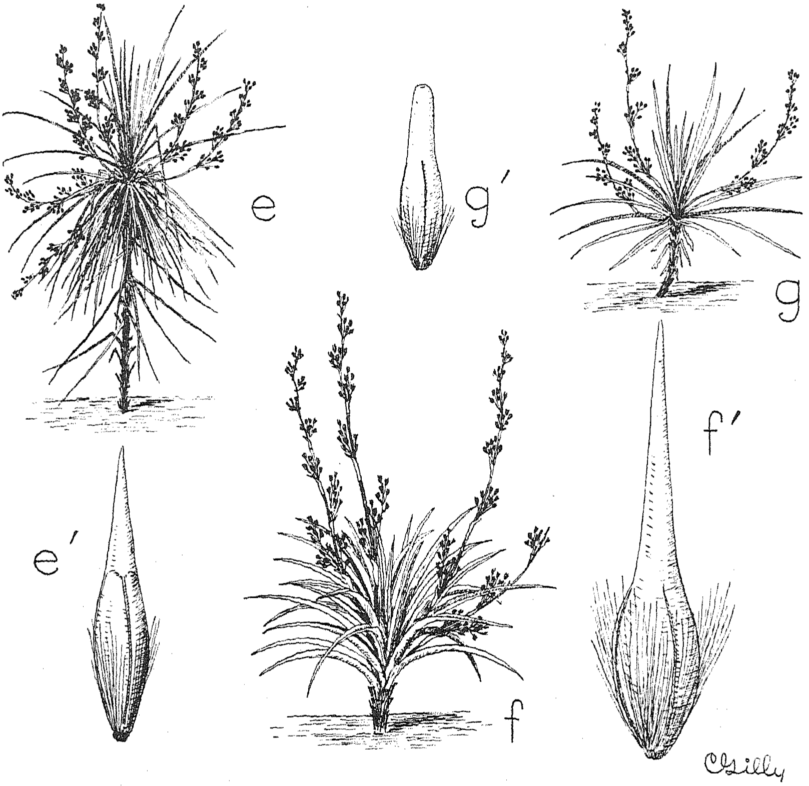

Fig. 3. *Everardia* (habit sketches ⅙ natural size; achenes × 10). *E. revoluta* Gilly; *e*, habit, *e′*, achene (drawn from *Tate 469*). *E. montana* Ridley; *f*, habit, *f′*, achene (drawn from *Tate 438*). *E. duidae* Gilly; *g*, habit, *g′*, achene (drawn from *Tate 638*).

Achene ovoid, dark brown, the tricarpellary markings faint, 2–3 mm. long, 1–2 mm. in diam., glabrous, tipped by a slender, glabrous, light brown beak half again as long as the body of the achene. Perianth scales very minute, orbicular or truncate; marginal cilia copious, appearing as a hypogynous ring of hairs, twisted, as long as or longer than the body of the achene. Stigmas 3, linear, from sub-terete to terete, somewhat inflated at their junction with the style proper, dark purple-brown, minutely pubescent. (Fig. 3, *f*, *f′*.)

Venezuela—bolivar: Mt. Roraima, the Ledge, Dec., 1884, *E. F. im Thurn 335* (type) (K); summit, 8600 ft., autumn 1898, *McConnell & Quelch 674* (K); 2500 m., Dec., 1909, *E. Ule 8543*, (K); summit, Nov. 27, 1927, *G. H. H. Tate 438* (NY).

7. **Everardia duidae** Gilly, sp. nov. Rhizomata simplicia, 2–4 mm. diam., ad 10 cm. alta, vaginis nigro-brunneis lacerato-fibratis tecta; folia 1–1.4 dm. longa, ad basim 5–8 mm. lata, infra glabra, supra granulato-asperata, margine arguto scabro; culmi floriferi laxe adscendentes, cum inflorescentibus ad 1.5 dm. alti; vagina ad basim 1.5–2 cm. longa; vaginae inflorescentiae minute cano-pubescentes; spiculae masculae ad 4 mm. longae, 1–1.5 mm. diam.,

glumis vacuis 4–6, ovatis vel lanceolatis mucronatis supra medium minute-pubescentibus, glumis staminibus 5–8, lanceolatis acutis glabris; spiculae foemineae 3 mm. longae, 1–1.5 mm. diam., glumis 5–6; achaenia glabra atro-brunnea, 1.2–1.7 mm. longa, 0.5 mm. diam.; rostro glabro truncato, corpus achaenii subaequante; squamellae hypogynae minutae orbiculares, ciliis paucis, quam corpore achaenii dimidio brevioribus.

Aerial rhizome simple, 2–4 mm. in diam., to at least 10 cm. tall, surrounded by blackish, ragged-fibrous leaf-sheaths. Leaves 1–1.4 dm. long, 5–8 mm. wide at the base, tapering gradually to the apex, glabrous on the under surface, granular-roughened above, flat for most of their length, slightly bicarinate at apex, margins sharp-scabrous, almost saw-edged. Flowering culms laxly ascending, flattened, densely appressed-pubescent, about 0.5 mm. wide, including inflorescence about 1.5 dm. high; basal sheath 1.5–2 cm. long. Inflorescence of 5–6 tufts of spikelets; sheaths of the inflorescence dark-brown, minutely hoary-pubescent, 4–10 mm. long, the leaf-like points as long as the sheaths. Staminate spikelets about 4 mm. long, 1–1.5 mm. in diam.; sterile glumes 4–6, from ovate to broadly lanceolate, mucronate, minutely pubescent above the middle; staminiferous glumes 5–8, lanceolate, acute, glabrous; stamens under each glume 4–8. Pistillate spikelets 3 mm. long, 1–1.5 mm. in diam., the glumes 5–6, ovate to lanceolate, mucronate, minutely pubescent to glabrate. Achene 1.2–1.7 mm. long, 0.5 mm. in diam., glabrous, dark brown, tapering into a blunt-truncated beak about as long as the body of the achene; beak glabrous, or sometimes minutely puberulent at the apex. Tricarpellary markings faint. Perianth scales minute, orbicular; marginal hairs few, about one-half as long as the body of the achene, straight or somewhat twisted. Stigmas linear, dark brown. (Fig. 3, *g*, *g′*.)

VENEZUELA—TERRITORIO AMAZONAS: Mt. Duida, summit of peak 7, 7100 ft., 1928–1929, *G. H. H. Tate 638* (TYPE) (NY).

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STUDIES ON AMERICAN HEPATICAE—I. REVISION OF THE GENUS THYSANANTHUS

MARGARET FULFORD

(WITH FIFTY-ONE FIGURES)

Three species of *Thysananthus*, a genus of the subgroup Holostipae of the Lejeuneae, have been reported from the Americas and a fourth is here proposed as new. Spruce[1] has described several species under *Lejeunea*, subgenus VIII, *Thysano-Lejeunea*, namely *L. amazonica* from the Amazon country, *L. dissoptera* from Guiana, and *L. pterobryoides* from Ecuador. In addition to these, Nees von Esenbeck[2] described a plant from Jamaica as *Phragmicoma Lehmanniana*, which Stephani later transferred to *Thysananthus*. Verdoorn[3] suggested that this plant was a *Caudalejeunea*. An examination of a portion of the type material shows that it is identical with *Caudalejeunea Lehmanniana* (Gottsche) Evans[4] and it should therefore be reduced to synonymy. Taylor[5] described plants collected in Ecuador by Professor W. Jameson under the name *Thysananthus mexicanus*. His plants do not have the characteristics of the genus *Thysananthus* as it has been delimited by recent monographers so that the species is a member of some other genus of the Lejeuneae.

The genus[6] as understood by Evans,[7] Verdoorn,[3] and others may be characterized as follows: the female inflorescence is terminal on the main stem or principal branch, with innovations proceeding from one or both sides below; the perianth is 3-angled in transverse section, with the ventral keel sharp and distinct; there are no secondary folds or ridges; carinal and surface wings are developed in some species; the female bracts and bracteoles, and the keels of the perianth are toothed to a greater or lesser degree; and the leaves and underleaves usually show some indications of teeth along the margins, particularly in the apical region.

The plants are large and grow in depressed mats or among other bryophytes on the trunks and bases of trees and over logs. The stem is robust and is differentiated into a prostrate primary caudex which is appressed to the substratum, and ascending or upright secondary stems which are usually abundantly branched. The branches are olive or dark green and often become deeply pigmented with brown.

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[1] Hepaticae of the Amazon and Andes. Trans. Bot. Soc. (Edinburgh) **15:** 105–110. 1884.

[2] In Gottsche, Lindenberg & Nees von Esenbeck, Syn. Hep. 302. 1845.

[3] Die Frullaniaceis XV. Die Lejeuneaceae Holostipae der Indomalaya unter Berücksichtigung sämtlicher aus Asien, Australien, Neu-seeland und Ozeanien angeführten Arten. XIII. *Thysananthus*. Ann. Bryol. Supl. **4:** 163–188. 1934.

[4] Hepaticae of Puerto Rico VIII. *Caudalejeunea*. Bull. Torrey Club **34:** 554–557. pl. 33. fig. 1–12. (1907.) 1908.

[5] On some new Musci collected by Professor W. Jameson on Pichincha. Hooker's Jour. Bot. 7: 187–199. 1848.

[6] For synonymy in the genus *Thysananthus* see Verdoorn, l. c.

[7] Hepaticae of Puerto Rico VIII. *Symbiezidium*, *Marchesinia*, *Mastigolejeunea*, *Caudalejeunea* and *Bryopteris*. Bull. Torrey Club **34:** 533–568. *pl. 31–33*. (1907.) 1908.

Evans[8] describes the secondary stem of *T. amazonicus* as being 3–8 cm. in length and about 0.15 mm. in diameter. The transverse section shows a uniform orange-brown pigmentation except for the slightly darker middle lamellae. The cortex is made up of 30–33 rows of thick-walled cells ranging from 10 to 20 μ in width, and from 10 to 15 μ in thickness. The cells of the medulla are quite similar, except that they have distinctly larger cell-cavities, so that the medulla appears somewhat more open than the cortex.

The branching of the subfloral innovations, other vegetative branches, and the male branches seem always to be of the *Radula* type.[9]

The lobule is small in proportion to the lobe. The keel is rounded and the upper edge, which is entire, tends to be tightly appressed to the lobe, so that a definite, inflated water-sac is usually formed. The apical tooth is from one to seven cells long and may be curved.

Although the genus, as indicated by the stem structure, is clearly a member of the Holostipae, which are characterized by entire underleaves, several species have retuse or distinctly bifid underleaves. Three of the American species show this characteristic. The additional generic characteristics are discussed under the descriptions of the separate species.

The writer wishes to acknowledge the helpful criticism of Dr. A. W. Evans of Yale University, and the courtesies extended by the New York Botanical Garden during the preparation of this paper.

The following abbreviations have been used to designate the location of specimens in the citations under the individual species: M, Missouri Botanical Garden; NY, New York Botanical Garden; and Y, Herbarium of Yale University, including the private collection of Dr. A. W. Evans.

KEY TO THE SPECIES

1. Underleaves obovate, rarely truncate, the apical margin serrate ...... 4. *T. comosus*
1. Underleaves subquadrate-cuneate, from retuse to deeply bifid.
    2. Lobule oblong, the tooth if present of only one or a few cells; leaf cells elliptical-angular in outline ...... 3. *T. amazonicus*
    2. Lobule more or less subquadrate, the tooth long, curved, of 5–7 cells; leaf cells quadrate in outline; underleaves distinctly bifid.
        3. Margins of the leaves and underleaves dentate with coarse teeth ...... 2. *T. pterobryoides*
        3. Margins of the leaves and underleaves from obscurely dentate to denticulate ...... 1. *T. Evansii*

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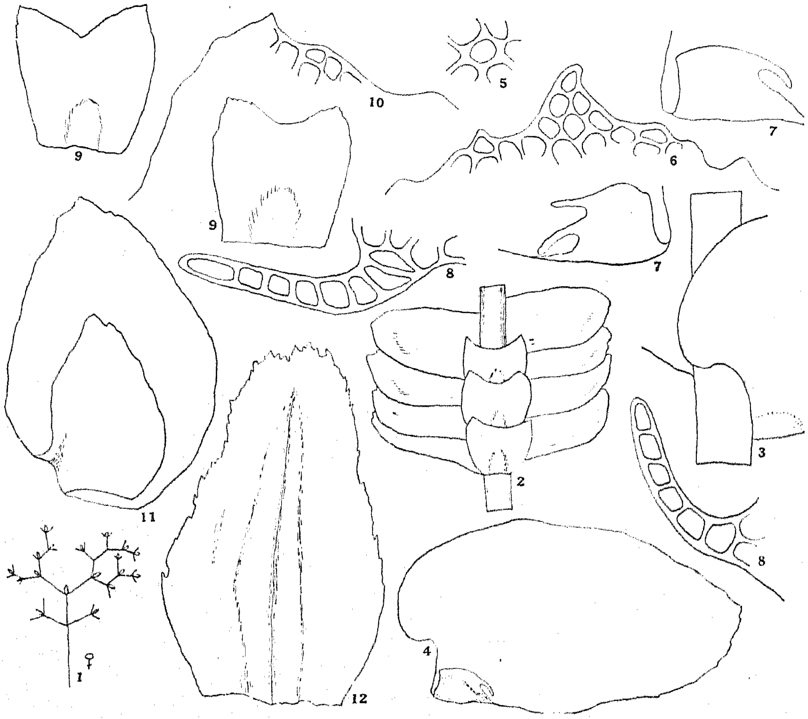
[8] Anatomy of the stem in the Lejeuneae. Bull. Torrey Club **62**: 187–214; 259–280. *8 fig.* 1935.

[9] For a description of the various types of branching see Evans, Branching in the Leafy Hepaticae. Ann. Bot. **26**: 1–37. *36 fig.* 1912.

Thysananthus Evansii Fulford, sp. nov. Caules robusti, olivacei, pinnate ramosi, feminini dichotomi; folia imbricata, divaricata, ovata, 1–1.3 mm. longa, superne obscure serrata, cellulis 8–10 μ diam., lobulo parvo, dente apicali longo; foliola imbricata, subquadrato-cuneata, bifida; flores dioici; bracteae femininae foliosae, lobulis magnis, planis, ovatis, bracteola magna, ovata, carinata, crasse dentata.

Plants robust, olive-green, becoming darker green in the older portions: secondary stems stout, to 4 cm. or more in length, with leaves to 2 mm. broad, ascending, irregularly pinnate, the branches obliquely spreading, the female branch system showing apparently regular dichotomy: leaf insertion curved in the upper part; the leaves imbricated, spreading, becoming a little deflexed when dry, unsymmetrically ovate, 1–1.3 mm. long, 0.5 mm. broad at the base, obscurely serrate above the middle, the dorsal base cordate, the ventral margin straight; the lobule small, inflated, ovate, 0.12 mm. long, 0.1 mm. high, the free margin entire, appressed, the apical region of the lobe 8–10 μ in diameter, cells of the base much longer, a vitta not differentiated, the cell walls uniformly thickened, the cell lumina rounded, trigones not evident, the



FIGS. 1–12. *T. Evansii* Fulford. FIG. 1. Diagram of the branching pattern of a female plant. FIG. 2. Portion of a plant, ventral view, × 15. FIG. 3. Portion of a leaf and stem, dorsal view, × 30. FIG. 4. A leaf, × 30. FIG. 5. A cell from the apical portion of a leaf, × 400. FIG. 6. Outline of the apical margin of a leaf, × 300. FIG. 7. Lobules, one of them has developed two apical teeth, × 90. FIG. 8. Apical teeth of lobules, × 400. FIG. 9. Underleaves, × 30. FIG. 10. Outline of the apical margin of a tooth of an underleaf, × 300. FIG. 11. Female bract, × 30. FIG. 12. Female bracteole, × 30. Drawn from the type material.

cuticle smooth to faintly verruculose: underleaves imbricated, attached in a straight line, subquadrate-cuneate, 0.7 mm. long, 0.5–0.6 mm. broad in the upper part, retuse or bifid to one-fifth the length, the broad and pointed divisions and the obtuse to lunulate sinus serrate, the lateral margins convex, entire, the cells as in the leaf: dioicous : female branches short, on the main stem or branches, always subtended by two subfloral innovations, a pair of leaves below the involucre intermediate in form between the bracts and the normal leaves; the bracts leaf-like in outline, 1 mm. or more long, the margins often more strongly serrate than in the leaf, the lobule ovate, much enlarged, plane, mostly 0.7 mm. long, the apical tooth not evident; the bracteoles broadly ovate, 1.3 mm. or more long, the margin coarsely dentate, the apex obscurely bifid, keeled nearly to the apex, the angle broad: male branches, perianths and sporophytes not seen.

Habitat: On bark of trees, lowland forests.

Distribution: British Honduras: Punta Gorda, without collector's name, TYPE (M).

The distinguishing characteristics of the species are its olive-green color and dichotomously branched female stems; the long, curved tooth of the lobule of the leaf; the bifid underleaves serrate above the middle; and the long, keeled, more or less bifid, dentate, female bracteoles. See figures 1–12.

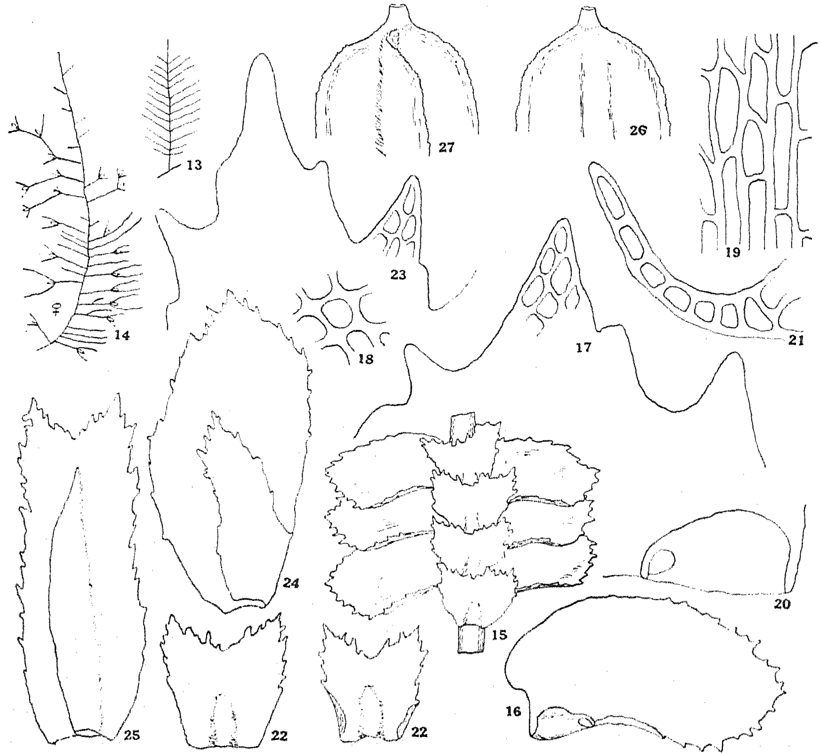
Thysananthus pterobryoides (Spruce) Stephani, Spec. Hep. **4**: 786. 1912. *Lejeunea (Thysano-Lejeunea) pterobryoides* Spruce, Trans. & Proc. Bot. Soc. Edinb. **15**: 109. 1884. *Bryopteris Wallisii* Stephani, Hedwigia **24**: 89. *pl. 1, fig. 1–8.* 1885. *Thysanolejeunea pterobryoides* Stephani (syn.), Spec. Hep. **4**: 786. 1912.

Plants olive green, becoming darker green in the older portions: secondary stems to 8 cm. or more in length, with leaves 2 mm. broad, ascending, more or less regularly and simply pinnate when sterile, inflorescences produced on primary branches of pinnate branch systems; leaf insertion curved in the upper part; the leaves imbricated, spreading, becoming a little deflexed when dry, 1–1.3 mm. long, 0.4–0.6 mm. broad at the base, unsymmetrically ovate, coarsely dentate above the middle, the dorsal base cordate, extending across the stem and beyond, the ventral margin more or less recurved, entire, the lobule inflated, ovate, 0.7–0.12 mm. long, 1.8–0.1 mm. high, the free margin appressed, entire, the apical tooth five to seven cells long, curved, the sinus deep, lunulate; the cells of the lobe averaging 8–10 μ in diameter, those of the basal area longer, a vitta not differentiated, the cell walls uniformly thickened, the cell lumina rounded, trigones not evident: underleaves imbricated, attached in a straight line, coarsely dentate, subquadrate-cuneate, 0.56–0.7 mm. long, 0.5–0.63 mm. broad in the upper part, bifid to one-fourth the length, the sinus lunulate, the teeth broad, acute, the cells as in the leaf: dioicous: female branches short, always with two subfloral innovations, a pair of leaves below the involucre intermediate in form between the bracts and normal leaves; bracts leaf-like in outline, to 1.3 mm. or more long, the lobule lanceolate, plane, more than half the length of the lobe, the apical tooth not evident, the lobe and lobule coarsely dentate above the middle; the bracteole oblong, to 1.5 mm. in length, bifid and coarsely toothed above the middle as in the underleaf, keeled nearly to the apex, the angle acute: perianth to 2.5 mm. long, the keels sharp, crenulate, occasionally serrate, the beak short: male branches and sporophytes not seen.

Habitat: On bark of trees in forests.

Distribution: COSTA RICA: San José, Lehmann, cited by Stephani.[10] PANAMA: Island of Coiba, *Seemann* (Y, NY). COLOMBIA: Cordoba, *Killip 11776, 11801* (Y, NY); without locality, *Wallace* (NY). ECUADOR: Pastaza River, *Spruce 1885, 109;* Manabi, *Wallis*, cited by Stephani (1885, 89), TYPE of *Bryopteris Wallisii*.

The distinguishing characteristics of the species are its olive-green color, the simply and regularly pinnate branching, the long apical tooth of the



FIGS. 13–27. *T. pterobryoides* (Spruce) Steph. FIG. 13. Diagram of branching pattern of a sterile stem. FIG. 14. Diagram of the branching pattern of a female stem. FIG. 15. Portion of a plant, ventral view, ×15. FIG. 16. A leaf, ×30. FIG. 17. Outline of the apical margin of a leaf, ×300. FIG. 18. A cell from the apical portion of a leaf, ×400. FIG. 19. Cells from the basal portion of a leaf, ×300. FIG. 20. A lobule, ×90. FIG. 21. An apical tooth of a lobule, ×400. FIG. 22. Underleaves, ×30. FIG. 23. Outline of the apical margin of a tooth of an underleaf, ×300. FIG. 24. Female bract, ×30. FIG. 25. Female bracteole, ×30. FIG. 26. Upper portion of a perianth, dorsal view, ×30. FIG. 27. Upper portion of a perianth, ventral view, ×30. Drawn from material collected by Dr. Killip in Colombia.

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[10] In Cryptogamae Centrali-Americanae. Hepaticae. Bull. Herb. Boiss. 2: 402–403. 1894.

lobule of the leaf, the bifid underleaves, and the coarsely dentate margins of the leaves and underleaves. See figures 13–27.

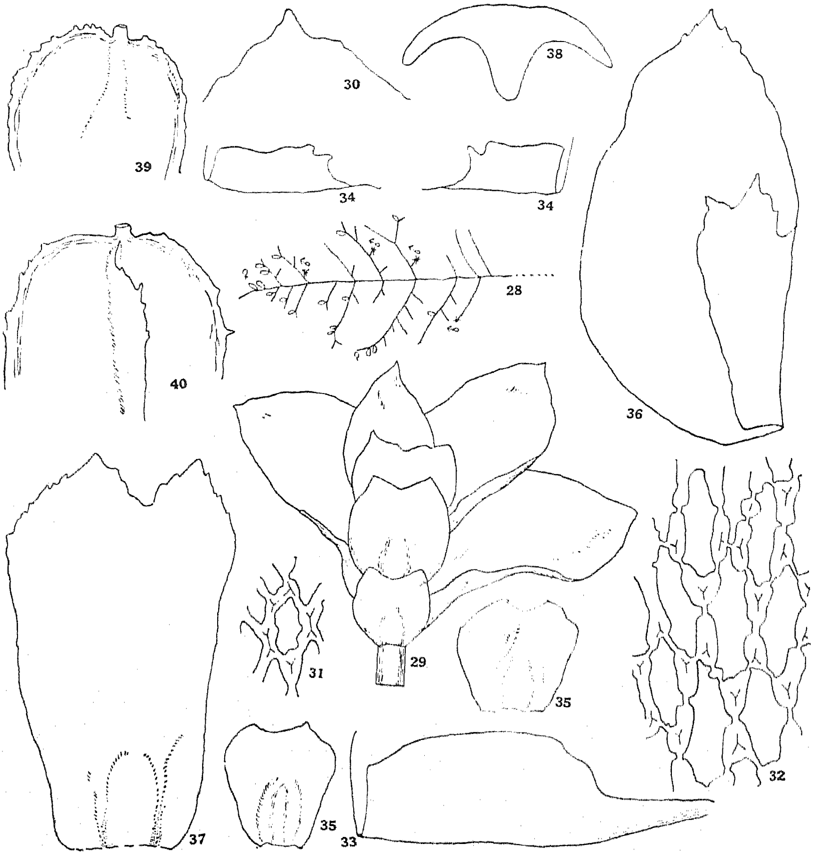
T. pterobryoides and *T. Evansii* have many characters in common, namely the color and size of the plants, the size of the leaves and underleaves, the size and shape of the leaf cells, the lobules of the leaves, and the production of pairs of subfloral innovations subtending the female inflorescences. They differ in that in *T. pterobryoides* the secondary stems are often very long, the branching is simply and regularly pinnate, and the female inflorescences are produced on primary branches of a pinnate branch system, while in *T. Evansii* the branches are less regularly pinnate and not so long, and the female plants always show an apparently regular dichotomy. (Compare figs. 13, 14 with fig. 1.)

The margins of the leaves and underleaves, and the female bracts and bracteoles of the two are strikingly different. (Compare figs. 15, 16, 17, 22–25 with figs. 2, 4, 6, 9, 10–12.) The shape of the female bracts is quite similar in the two species, but the bracteoles of *T. Evansii* are broadly ovate and the angle of the keel is broad, while in *T. pterobryoides* the bracteoles are oblong and the angle of the keel is acute. Unfortunately no perianths have been found in *T. Evansii*, so that a comparison of this structure in the two species cannot be made at this time.

Not only do *T. pterobryoides* and *T. Evansii* have many characteristics in common but they also make up a unit within the genus which is different not only from the other South American forms but also from any of the Asiatic species with which I am familiar. All the other species have a deep brown pigmentation and have large leaf cells which are more or less elongate and hexagonal or angular-elliptical in outline, with conspicuous trigones, and often additional intermediate thickenings.

THYSANANTHUS AMAZONICUS (Spruce) Stephani, Spec. Hep. **4**: 784. 1912. *Lejeunea* (*Thysano-Lejeunea*) *amazonica* Spruce, Trans. Bot. Soc. Edinb. **15**: 106. 1884. *Thysanolejeunea amazonica* Stephani (syn.) l.c.

Plants dark greenish brown, becoming very dark brown in the older portions; secondary stems coarse, 6 cm. or more in length, with leaves to 3 mm. broad, irregularly pinnate, the branches oblique, often branched, female branches with only one subfloral innovation: leaf insertion curved in the upper parts; the leaves imbricated, spreading, tightly appressed to the stem when dry, averaging 1.4–1.6 mm. long, 0.8 mm. broad at the base, unsymmetrically ovate, entire except for an occasional serration, the dorsal base cordate, covering the stem and extending beyond, the ventral margin entire, recurved; the lobule small, inflated, oblong in outline, 0.3–0.42 mm. long, 0.15 mm. high, the free margin entire, appressed, the apical tooth sometimes evident, of one or two cells, the slime papilla not seen, the sinus shallow, lunulate; cells of the marginal and apical region and of the lobule 16–20 μ × 8 μ, those of the base longer, a vitta not differentiated, the cell walls thin, the trigones conspicuous, with convex sides, soon becoming confluent through the deposition of secondary material, intermediate thickening frequent, the cell lumina angular-oblong in outline, the cuticle smooth to verruculose: underleaves imbricated, attached in a straight line, cuneate, retuse to shortly bifid, averaging 0.77 mm. long, 0.7 mm. broad in the upper part, the teeth very short and broad, the sinus shallow, lunulate, the margins entire, sometimes obscurely serrate on underleaves near the tip of the stem, the cells as in the leaf: autoicous: male inflorescences terminal on short lateral branches, the bracts in two to four pairs, at the tip of a branch, imbricated, the lobe broadly ovate, the lobule ovate, smaller, the apical tooth conspicuous, the margins sparsely dentate; the bracteoles imbricated, similar to the underleaves; antheridia in pairs: female branches short, occurring singly or several approxi-



Figs. 28–40. *T. amazonicus* (Spruce) Steph. Fig. 28. Diagram of branching pattern of a stem. Fig. 29. Portion of a plant, ventral view, × 15. Fig. 30. Portion of the apical margin of a leaf, × 30. Fig. 31. A cell from the apical portion of a leaf, × 400. Fig. 32. Cells from the basal portion of a leaf, × 300. Fig. 33. Lobule, × 90. Fig. 34. Lobules, × 30. Fig. 35. Underleaves, × 15. Fig. 36. Female bract, × 15. Fig. 37. Female bracteole, × 15. Fig. 38. Outline of a cross section of the perianth. Fig. 39. Upper portion of a perianth, dorsal view, × 30. Fig. 40. Upper portion of a perianth, ventral view, × 30. Drawn from type material.

mate, appearing lateral, a subfloral innovation from only one side, the bracts similar in outline to the leaves, averaging 2 mm. long, the lobule oblong, ovate, plane, 0.8 mm. long, the margins of both coarsely toothed in the upper part; the bracteole oblong, bifid, 1.6 mm. or more in length, averaging 0.9 mm. broad in the upper part, the teeth broad, acute, the sinus acute, the margins of the teeth serrate and coarsely dentate: perianth to 2 mm. long, the beak short, the keels serrate and dentate with scattered teeth: sporophyte not seen.

Habitat: On bark of trees in forests.

Distribution: TRINIDAD: Mora Forest, *E. G. Britton 2878* (Y, NY); without locality, *Fendler* (NY). COLOMBIA: Without locality, *Wier* (NY). BRAZIL: Pará, Spruce, Hepat. Spruc., TYPE (Y, NY). BRITISH GUIANA: near Bartica, *Richards 188, 510* (Y).

The distinguishing characteristics of the species are the large, coarse, irregularly branched, dark greenish brown stems; the large, ovate, entire leaves with oblong lobules which have a 1–3-celled apical tooth; the long-angular cell lumina, large trigones and intermediate thickenings; and the large cuneate underleaves which are retuse or somewhat bifid at the apices. See figures 28–40.

T. amazonicus is readily distinguished from the preceding species because of its autoicous inflorescence, the deep brown pigmentation, the entire margins of the leaves and underleaves, the short apical tooth of the lobule, and the angular-oblong outline of the leaf cells.

THYSANANTHUS COMOSUS Lindenberg, in Lehmann Pug. Pl. **8**: 25. 1844. *Lejeunea comosa* Mitten, Jour. Linn. Soc. Bot. **5**: 109. 1861. *Lejeunea* (*Thysano-Lejeunea*) *comosa* Spruce, Trans. Bot. Soc. Edinb. **15**: 108. 1884. *Thysananthus dissopterus* Stephani, Spec. Hep. **4**: 784. 1912. *Thysanolejeunea dissoptera* Stephani (syn.) l.c.

Plants dark greenish brown, becoming very dark brown in the older portions; stems coarse, 5 cm. or more in length, with leaves to 2.5 mm. broad, irregularly pinnate or bipinnate, microphyllous branches frequent, female branches with only one subfloral innovation: leaf insertion curved in the upper part; the leaves imbricated, spreading, ascending and appressed to the stem when dry, averaging 1.4 mm. long, 0.85 mm. broad at the base, unsymmetrically ovate, entire except for an occasional serration, the dorsal base cordate, covering the stem and extending beyond, the ventral margin entire, recurved: the lobule small, inflated, ovate in outline, 0.3–0.4 mm. long, 0.2 mm. high, the free margin entire, appressed, the apical tooth one to several cells long, the inner (proximal) tooth sometimes evident, of one or two cells, the sinus very shallow; cells of the lobule and the margin and apical regions averaging 20 μ long, 12 μ wide, those of the base longer, a vitta not differentiated, the cell walls thin, the trigone conspicuous, with convex sides, often becoming coalesced, intermediate thickenings frequent, the cell lumina angular-oblong in outline, the cuticle smooth or faintly verruculose: underleaves imbricated, attached in a straight line, obovate to cuneate, averaging 0.7 mm. long, 0.7 mm. broad in the upper part, the margin serrate, the cells as in the leaf: autoiceous (?) or dioicous: female branches short, occurring singly, with one subfloral innovation, thus appearing lateral, the bracts similar in outline to the leaves, averaging 1.3 mm. long, the ventral margin dentate, the lobule large, 0.85 mm. long, plane, more or less obovate, obscurely bifid, the margins dentate; the bracteole cuneate, similar to the underleaf, 0.9–1.2 mm. long, the margins serrate and coarsely dentate: the perianth mostly 1.5 mm. long, the beak short, the keels densely set with large irregularly tooth laciniae, the dorsal face smooth, the ventral faces each with one or more groups (in one or two rows) of laciniae similar to those of the keels: male branches and sporophytes not seen.

Habitat: On bark of trees in forests.

Distribution: GUIANA: Hb. Hooker, (Y, NY). BRAZIL: Tauau, Spruce (NY). Also in the Indo-Malayan Region.

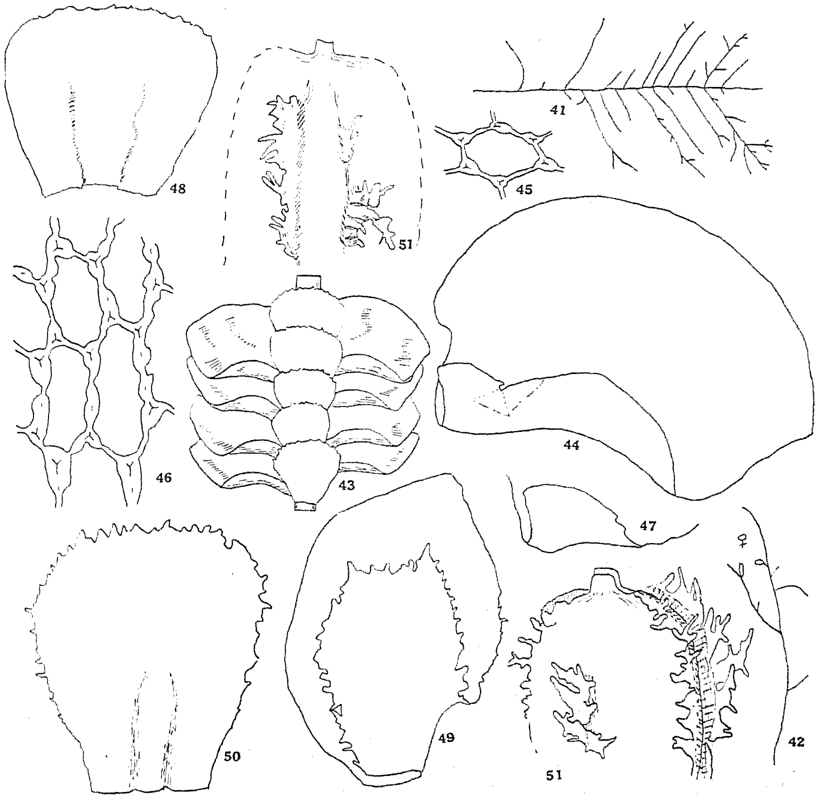
The distinguishing characteristics of the species are its robust habit, dark color, the nearly entire leaves, and small lobules with a short apical tooth; the long-angular cell lumina and conspicuous trigones; the obovate underleaves serrate along the upper margins; and the laciniate wings of the perianth. See figures 41–51.

T. amazonicus and *T. comosus* are very similar in many respects, namely, size of plant, growth habit, and, in a general way, the shape of the leaf and of the leaf cells. The underleaves of *T. comosus*, when well developed, are obovate with a serrate margin (figs. 43, 48), while in *T. amazonicus* (figs. 29, 35), although they are more or less obovate, the apical region is distinctly retuse or more or less 2-toothed. The apical margin is serrate to a greater or lesser degree.

An additional striking distinction is to be found in the parts of the female involucres of the two species. The bracts of *T. amazonicus* are dentate at the apices, and the lobules are long, narrow, and conspicuously bifid with the margins occasionally toothed in the upper part (fig. 36), while those of *T. comosus* are dentate along the ventral margins, and the lobules are long, ovate, obscurely bifid, with the margins coarsely dentate to the base (fig. 49). The bracteoles of *T. amazonicus* are oblong, bifid, and coarsely dentate in the upper part, while those of *T. comosus* are cuneate, and from serrate to dentate throughout. (Compare figs. 37 and 50.) The laciniate wings on the keels of the perianths of *T. comosus* will immediately distinguish that species from *T. amazonicus*, in which the perianth keels are only sparingly dentate (figs. 39–40, 51).

The leaves and underleaves in the vicinity of the female branches and sometimes at the tips of the stems are usually more strongly toothed than elsewhere on the plant. When toothed leaves occur in the region of the female branches they are intermediate in form between ordinary leaves and the bracts and bracteoles.

All the South American material examined was dioicous. Spruce describes the South American material (under *Thysano-Lejeunea dissoptera*)



FIGS. 41–51. *T. cosmos* Lindenb. FIG. 41. Diagram of branching pattern of a sterile stem. FIG. 42. Diagram of branching pattern of a female plant. FIG. 43. Portion of a plant, ventral view, ×15. FIG. 44. A leaf, ×30. FIG. 45. A cell from the apical portion of a leaf, ×400. FIG. 46. Cells from the basal portion of a leaf, ×300. FIG. 47. Lobule, ×30. FIG. 48. Underleaf, ×30. FIG. 49. Female bract, ×15. FIG. 50. Female bracteole, ×30. FIG. 51. Ventral faces of a perianth, ×30. Drawn from the original collection from Guiana.

as "dioica (?)"; Stephani[11] describes both *T. dissopterus* and *T. comosus* as "dioicous," while Verdoorn's description[12] states that the species is "usually monoicous." The portion of the type material from Paulo-Penang which I examined had many well developed perianths but I could find no male branches.

There has been some difference of opinion as to whether the South American plants were actually *T. comosus*, a species widespread in Indo-Malaya. Lindenberg in the original description cited plants in "Paulo Penang, ubi legit cel. Wallich," also "in Guiana lectam accepi ab illustr. Hooker." Spruce[13] considered this interpretation to be incorrect and separated the

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[11] Spec. Hep. **4:** 784, 787. 1912.

[12] Verdoorn, op. cit. p. 176.

[13] Trans. Bot. Soc. Edinb. **15:** 107–109. 1885.

South American plants from the "composite species," *T. comosus*, and called the South American plants *Lejeunea (Thysano-Lejeunea) dissoptera.* He also described the material from Paulo Penang, retaining for it the specific epithet *comosus.* On the other hand, Mitten[14] considered the two to be identical. Stephani's comments[15] concerning the Guiana material are obscure, for he says (discussing *T. comosus*), that only Nos. 85 and 86 represent the true species, moreover the American No. 84 is very similar. Verdoorn[16] has followed Lindenberg in considering the South American and the Asiatic material identical. In my observations of a portion of the type material from both Guiana and Paulo-Penang in the Mitten collection I have not been able to discover any variations of sufficient degree and uniformity by which the two could be separated. The two seem to be identical. Except for the original material from Guiana, I have seen only one other collection from South America, one made by Spruce at Tauau, Brazil. Spruce makes no mention of this collection in his "Hepaticae of the Amazon and Andes."

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[14] Hepaticae Indiae Orientalis. Jour. Linn. Soc. Bot. **5**: 89–128.

[15] Die Gattung *Lejeunea* im Herbarium Lindenberg. Hedwigia **29**: 1–23, 1890.

[16] Verdoorn, op. cit. 175.

NEW RUSTS FROM AMERICA AND AFRICA[1]

GEORGE B. CUMMINS[2]

(WITH SEVEN FIGURES)

Puccinia makenensis Cummins, sp. nov. (Fig. 3.) Pycniis non visis. Aeciis hypophyllis, in maculis flavidis non vel leniter incrassatulis 1–5 mm. diam. aggregatis vel plus minusve sparsis, cupulatis, 0.2–0.25 mm. diam.; cellulis peridii angulariter globoideis vel ellipsoideis vel polyhedricis, 14–20 × 16–26 μ, pariete interiore verrucoso 3–3.5 μ cr., exteriore striato 4–5 μ cr.; aeciosporae globoideae vel ellipsoideae, 13–17 × 17–20 μ; membrana hyalina, 0.5–1.0 μ cr., minuteque verruculosa. Urediis nullis. Teliis amphigenis vel plerumque epiphyllis, irregulariter aggregatis, rotundatis vel elongatis, usque ad 1.5 mm. longis, atro-brunneis, subepidermalibus, plus minusve indehiscentibus, loculatis, paraphysibus brunneis coalitis numerosis; teliosporae variabiles sed plerumque clavatae, ad apicem rotundatae, attenuatae vel obtusae, deorsum attenuatae, medio leniter constrictae, 19–27 × (40–)48–66(–75) μ; membrana 1.5–2.5 μ cr., ad apicem 3–8 μ cr., castaneo-brunnea, levi; pedicello persistenti, sporam aequante, flavido.

On *Blepharis boerhaaviaefolia* (*maderaspatensis*), Makene, Sierra Leone, Jan. 28, 1939, *F. C. Deighton 1741.* TYPE in the Arthur Herbarium and in the Herbarium of the Imperial Mycological Institute.

The aecia and teliospores are similar to those described for *Puccinia blepharidis* P. Henn., although the teliospores are somewhat longer, but the loculate, paraphysate telia of *P. makenensis* are distinctive. It is probable that *Aecidium blepharidis* Pat. & Har., which occurs on the same host, is synonymous with *P. makenensis.*

Puccinia multiloculata Cummins, sp. nov. (Fig. 1.) Pycnia epiphylla, subepidermalia, globosa, 100–150 μ diam.; perpauca vel frequenter non visa. Aecia hypophylla, subepidermalia, dense aggregata in maculis 1–2 mm. diam., breviter cupulata, 0.15–0.25 mm. diam.; cellulis peridii rhomboideis vel oblongo-ellipsoideis, 14–20 × 23–30 μ, pariete interiore verrucoso 2.5–3 μ cr., exteriore striato 4–5 μ cr.; aeciosporae globoideae, 13–16 × 15–18 μ; membrana hyalina, 0.5 μ cr., sublevi. Uredia ignota, verissimiliter nulla. Telia petiolicola, elongata, usque ad 7 mm. longa, atra, subepidermalia, indehiscentibus, loculata, paraphysibus numerosis brunneis coalitis; teliosporae (rarius 2-septatae) clavatae vel cylindraceae, ad apicem rotundatae, truncatae vel attenuatae, ad basim attenuatae, medio leniter constrictae, 13–19 × 36–62 μ; membrana pallide castaneo- vel aureo-brunnea, 1.5 μ cr., ad apicem 3–6 μ cr., levi; pedicello persistenti, sporam aequante, intense brunneolo.

On *Thunbergia cynanchifolia,* Segbwema, Sierra Leone, Dec. 11, 1937,

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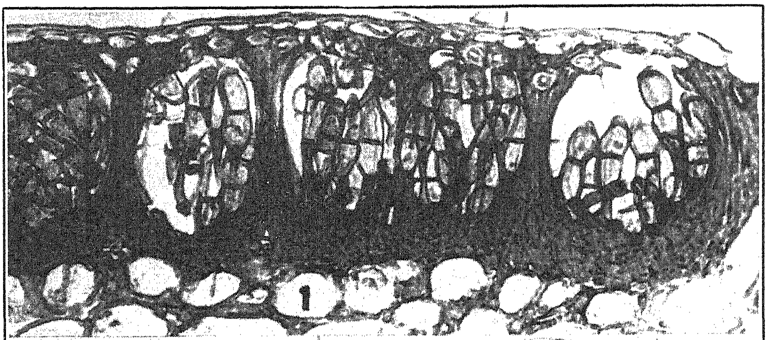
[1] Contribution from the Department of Botany, Purdue University Agricultural Experiment Station, Lafayette, Indiana.

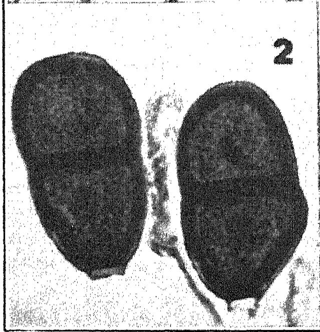
[2] I am indebted to Dr. G. R. Bisby, Imperial Mycological Institute, Kew, England, Mr. H. E. Parks, Trinidad, Calif., and Dr. John A. Stevenson, Bureau of Plant Industry, Washington, D. C., who made available for study certain of the specimens reported here.

F. C. Deighton 1460. TYPE in the Arthur Herbarium and the Herbarium of the Imperial Mycological Institute.

This species is distinct from other species of *Puccinia* on *Thunbergia* because of the loculate, paraphysate telia. The pedicel of the teliospores is usually darker than the base of the spore. It is doubtful, judging from descriptions, if the aecia are distinguishable from those of *P. thunbergiae* Cooke and *P. tandaaiensis* Hopkins. Only one telial group was seen but the telia are probably not always confined to the petioles.

Puccinia paroselae Cummins, sp. nov. (Fig. 2.) Urediis hypophyllis vel caulicolis, subepidermalibus, sparsis, rotundatis vel oblongis, 0.4–1.2 mm. longis, cinnamomeis; urediosporae obovoideae, ellipsoideae vel late ellipsoideae, 15–20 × 20–29 (–33) μ; membrana 1.5 μ cr., cinnamomea, minuteque echinulata, poris germ. 3 vel 4, aequatorialibus vel plus minusve sparsis. Teliosporae in uredia ellipsoideae vel oblongo-ellipsoideae, utrinque ro-





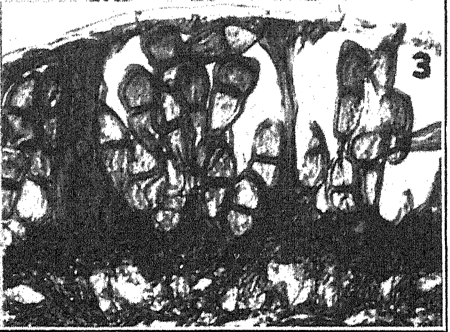


FIG. 1. Photograph of a free-hand, unstained section of the loculate telium of *Puccinia multiloculata,* showing the abundant development of the brown paraphyses and the concolorous, subjacent, stroma-like tissue. × 240.

FIG. 2. Two teliospores of *Puccinia paroselae;* note that the pore of the upper cell is approximately apical while that of the lower cell is near the short, fragile pedicel. × 800.

FIG. 3. Photograph of a free-hand, unstained section of the telium of *Puccinia makenensis,* showing the brown paraphyses which divide the sorus into locules. × 240.

tundatae vel ad basim leniter attenuatae, medio leniter constrictae, 21–25 × 35–42(–45) μ; membrana 2–2.5 μ cr., pallide castaneo- vel aureo-brunnea, minuteque verrucosa; poro superiore apicali vel subapicali, inferiore infra medium loculum sito; pedicello hyalino, fragili, brevissimo.

On *Parosela mollis*, roadside in Santa Rosa Canyon, Riverside Co., Calif., Feb., 1940, *H. E. Parks* & *Marvin Jordan 6430*. TYPE in the Arthur Herbarium.

According to the relationship of the host one would expect this rust to belong in the genus *Uropyxis* but the presence of only a single germ pore in each cell of the teliospore excludes it from that genus.

Puccinia puritanica Cummins, sp. nov. (Fig. 4.) Urediis hypophyllis, subepidermalibus, sparsis, rotundatis vel oblongis, 0.3–0.8 mm. longis, pallide cinnamomeis; urediosporae late ellipsoideae, ellipsoideae vel obovoideae, 16–20 × 20–25 μ; membrana 1.5 μ cr., pallide cinnamomea, minuteque echinulata; poris germ. 2, superaequatorialibus. Teliis conformibus; teliosporae clavatae vel oblongae, ad apicem rotundatae, deorsum attenuatae, medio constrictae, 12–17 × 25–37(–40) μ; membrana 1–1.5 μ cr., ad apicem 4–8 μ, flavida vel pallide aureo-brunnea, levi; pedicello hyalino, sporam subaequante vel breviori. Statim germ.

On *Carex pennsylvanica*, Waltham, Mass., Oct. 1, 1910, *A. B. Seymour 10*. TYPE in the Arthur Herbarium and in the Mycological Collections of the Bureau of Plant Industry, U. S. Department of Agriculture.

The urediospores of this rust are indistinguishable from those of *Puccinia extensicola* Plowr. or of *Uromyces perigynius* Halst. Telia of the latter species are also present in this specimen and, while some of the uredia may belong with them, sectioning proved that the nearly colorless teliospores of *P. puritanica* occur in the uredia as well as in separate sori. The similarity of the uredia of the two species, the close association of the two kinds of telia and the fact that the two-celled teliospores germinate at once lead to the speculation that perhaps a single species was present, with the *Uromyces* spores representing the resting stage. Such a life cycle would be unique but possibly could occur. However, numerous sections of the telia failed to reveal mixture of the one- and two-celled teliospores.

The relationship of *P. puritanica* is uncertain. While the urediospores are like those of *P. extensicola* the teliospores show no similarity but are near those of the Philippine species, *P. constata* Syd.

Uromyces ictericus Cummins, sp. nov. (Fig. 5.) Pycniis ignotis. Aeciis epiphyllis, subepidermalibus, aggregatis in maculis pallidis 2–4 mm. diam., aperidiatis, poro apertis; aeciosporae catenulatae, globoideae, ellipsoideae vel oblongo-ellipsoideae, 16–23 × 20–30 μ; membrana 1–1.5 μ cr., hyalina vel pallide flavida, verrucosa. Urediis nullis. Teliis hypophyllis, subepidermalibus, aggregatis, rotundatis, oblongis vel confluentibus, pulvinatis, cinnamomeis vel flavidis; teliosporae late ellipsoideae, ovoideae vel obovoideae, 15–20 × 20–30 μ; membrana 1.5–2 μ cr., ad apicem 3–5 μ cr., flavidula vel

hyalina, levi; pedicello persistenti, hyalino, sporam aequante vel longiore.

On *Iresine celosia*, Aguas Amargas, Quezaltenango, Gautemala, Jan. 30, 1917, *E. W. D. Holway 803*, TYPE; Solola, Guatemala, Jan. 28, 1915, *Holway 141*. Type in the Arthur Herbarium.

These collections have previously been assigned to *Uromyces iresines* Lagerh., a South American species which has similar aecia but larger (23–30 × 27–40 μ) aeciospores with thicker walls (1.5–2.5 μ) and ovoid, larger teliospores (18–24 × 33–44(–47) μ). The teliospores are similar to those of *Uromyces clarus* Jacks & Holw., a species possessing uredia with striate urediospores.

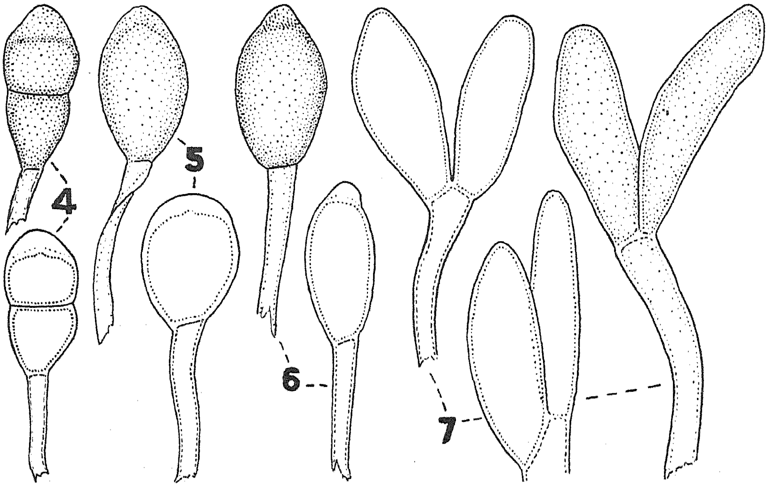


FIG. 4. Two teliospores of *Puccinia puritanica*. × 650.

FIG. 5. Two teliospores of *Uromyces ictericus*, a Guatemalan species previously confused with the South American *U. iresines* Lagerh. × 650.

FIG. 6. Two teliospores of *Uromyces necopinus*, a species previously included in the demicyclic *U. affinis* Wint. × 650.

FIG. 7. Teliospores of *Ypsilospora baphiae*, a rust in which the teliospores are borne in laterally free pairs on a common pedicel. × 650.

Uromyces necopinus Cummins, sp. nov. (Fig. 6.) Urediis incertis; urediosporae obovoideae vel late ellipsoideae, 17–20 × 20–29 μ; membrana cinnamomeo-brunnea, 1.5 μ cr., minuteque echinulata; poris germ. 3, aequatorialibus. Teliis amphigenis, subepidermalibus, sparsis vel plus minusve aggregatis, rotundatis, 0.2–0.5 mm. diam., pulvinatis, cinnamomeis; teliosporae ovoideae, ellipsoideae vel oblongae, 10–18 × 25–36 μ; membrana 1–1.5 μ cr., ad apicem 5–7 μ cr., pallide aureo-brunnea vel flavida, levi; pedicello persistenti, hyalino, sporam aequante vel longiore.

On *Hypoxis hirsuta*, vicinity of Lake Katrine, Ulster Co., N. Y., Aug. 17, 1916, *P. Wilson 402*, TYPE; Norwich, Conn., Aug. 17, 1889, *W. A. Setchell*. Type in the Arthur Herbarium.

Uromyces necopinus has been confused with *U. affinis* Wint. from which it is readily separable because of its smooth teliospores.

Jackson (Mycologia **18**: 157. 1926) has pointed out that *Uredo hypoxidis* (Bres.) P. Henn. should not be considered as synonymous with *U. affinis. U. affinis* was originally described as lacking uredia and there is no present evidence to contradict this. In fact, Demetrio's original collection is the only specimen in the Arthur Herbarium.

Ypsilospora Cummins, gen. nov. (*Pucciniaceae.*) Pycnia subcuticularia, hemispherica vel conoidea. Aecia et uredia nulla vel adhuc ignota. Telia subepidermalia; teliosporae unicellulares inter se liberae, binae in apice pedicello communi natae, hyalinae vel subhyalinae, statim germinantes ad apicem in promycelium typicum elongatae.
TYPE SPECIES: *Ypsilospora baphiae.*

Ypsilospora baphiae Cummins, sp. nov. (Fig. 7.) Pycnia subcuticularia, hemisphaerica vel conica, maculis incrassatulis usque ad 7 mm. diam. occupantibus. Aecia et uredia nulla. Telia subepidermalia, plus minusve profunde immersa, amphigena, inter pycnia sparsa, rotundata, 0.15–0.25 mm. diam. vel confluentibus, flavida; teliosporae cylindraceae vel oblongo-ellipsoideae, 11–15 × 34–50 μ; membrana hyalina, 1 μ cr. vel ad apicem 2 μ cr., levi; pedicello hyalino, persistenti vel fragili, sporae aequante vel breviore.
On *Baphia nitida*, Maboma, Sierra Leone, Nov. 5, 1939, *F. C. Deighton 2138.* TYPE in the Arthur Herbarium and in the Herbarium of the Imperial Mycological Institute.

This interesting microcyclic rust has 1-celled teliospores borne in pairs at the apex of a common pedicel. The pedicels disjoin from the sorus, the mature spores are pushed upward by the development of younger spores below and accumulate above the sorus. The arrangement of two teliospores upon a common pedicel is similar to that which characterizes the teliospores of *Sphenospora*, except that here the two spores have no common wall. It should be noted that the teliospores of *Sphenospora copaiferae* (P. Henn.) Syd. are described (Monogr. Ured. **4**: 584. 1924) as ". . . am Septum meist ziemlich tief eingeschnürt. . . ." *Copaifera* is likewise a genus of the Leguminosae and the two rusts may prove to be closely related.

Uredo aspiliae-latifoliae Cummins, sp. nov. Uredia hypophylla, subepidermalia, rotundata, 0.2–0.4 mm. diam., pulverulenta, cinnamomea; periphysibus inconspicuis, cylindraceis vel ampullaceis, 8–14 × 30–50 μ, membranis 1 μ cr., ad apicem 1.5–3 μ cr., pallide brunneis; urediosporae ellipsoideae, obovoideae vel globoideae, 17–23 × 19–27 μ; membrana 1.5 μ cr., cinnamomeo-brunnea, moderate echinulata; poris germ. 2, aequatorialibus.
On *Aspilia latifolia*, Kenema, Sierra Leone, Dec. 5, 1937, *F. C. Deighton 1505.* TYPE in the Arthur Herbarium and in the Herbarium of the Imperial Mycological Institute.

This species differs from previously described rusts on *Aspilia* by the presence of paraphyses in the uredia.

Aecidium brideliae-micranthae Cummins, sp. nov. Pycnia epiphylla, subepidermalia, globosa, 120–150 μ diam., paraphysata. Aecia hypophylla, subepidermalia, dense aggregata in maculis atro-brunneis usque ad 15 mm. diam., flavida, breviter cupulata, 0.15–0.2 mm. diam.; cellulis peridii fragilis, plus minusve isodiametricis, 15–20 μ diam., minuteque verruculosis; aeciosporae globoideae, 10–15 μ diam.; membrana 0.5 μ cr., hyalina, minuteque verruculosa.

On *Bridelia micrantha*, Ngelehun, Sierra Leone, Apr. 19, 1940, *F. C. Deighton 2269.* TYPE in the Arthur Herbarium and in the Herbarium of the Imperial Mycological Institute.

Aecidium cynanchi Cummins, sp. nov. Pycniis epiphyllis, globosis, 80–110 μ diam., subepidermalibus, paucis. Aeciis hypophyllis, laxe aggregatis in maculis pallidis usque ad 12 mm. diam., cupulatis, margine revoluto; cellulis peridii angulariter globoso vel oblongo, 14–20 × 19–25 μ; pariete interiore verrucoso 3 μ cr., exteriore levi 2 μ; aeciosporae globoideae vel ellipsoideae, 12–17 × 14–18 μ; membrana 1 μ cr. hyalina, minuteque verruculosa.

On *Cynanchum manni*, Nganyahun, Sierra Leone, Apr. 19, 1940, *F. C. Deighton 2270.* TYPE in the Arthur Herbarium and in the Herbarium of the Imperial Mycological Institute.

Aecidium leonense Cummins, sp. nov. Pycnia non visa. Aecia caulicola, ubique aequaliter denseque distributa, totam superficiem occupantia, subepidermalia, breviter cupulata, 0.2–0.3 mm. diam.; cellulis peridii plus minusve laxe conjunctis, rhomboideis, 13–16 × 15–19 μ, pariete interiore moderate verrucoso 3 μ cr., exteriore 3–3.5 μ cr. levi; aeciosporae globoideae vel oblato-sphaeroideae, 11–16 × 11–15 μ; membrana hyalina, 1 μ cr., minuteque verruculosa.

On *Dioscorea* sp., Sembehun, Sierra Leone, Apr. 26, 1940, *F. C. Deighton 2282.* TYPE in the Arthur Herbarium and in the Herbarium of the Imperial Mycological Institute.

Notes by the collector of this systemic rust are as follows: "Causing a witch-broom with thickening of the attacked stems. From appearance, very possibly a perennial rust."

THE ARTHUR HERBARIUM,
PURDUE UNIVERSITY AGRICULTURAL EXPERIMENT STATION.

STUDIES IN THE FAMILY WORONINACEAE—I. DISCUSSION OF A NEW SPECIES INCLUDING A CONSIDERATION OF THE GENERA PSEUDOLPIDIUM AND OLPIDIOPSIS

D. A. McLarty

(WITH TWENTY-SIX FIGURES)

INTRODUCTION

The genus *Olpidiopsis* was established by Cornu in 1872 to include five species which he found parasitizing various members of the Saprolegniales. For three of these species Cornu described thick-walled resting spores with one or several attached empty cells which he assumed were antheridia. Although he did not mention it specifically as a generic character, this "cellule adjacente," which Cornu observed in only three of his five species, came to be regarded as the distinguishing character of the genus. In 1878 Reinsch observed the passage of the contents of the smaller into the larger thallus, and since that time the resting spores of *Olpidiopsis* have been generally considered to arise as the result of definite sexual fusions.

A few years later, however, Fischer (1880) failed to observe antheridial cells in what he considered to be *O. Saprolegniae*. Accordingly in 1882 he rejected the "adjacent cell" character as diagnostic for the genus and restricted *Olpidiopsis* to species which produce asexual resting spores. Subsequent studies, however, convinced Fischer that his earlier observations had been incorrect, and in 1892 he restored the genus to its original status and established a second genus, *Pseudolpidium*, to include *Olpidiopsis*-like species with asexual resting spores. In his genus Fischer included *P. Saprolegniae* and *P. fusiforme*, for which he described resting spores, and four additional very dubious species for which no resting spores were observed.

Since the time of Fischer no critical work has been done on the species which he observed but many new species of *Olpidiopsis* and *Pseudolpidium* have been described, and generic distinctions have been made solely upon the basis of the presence or absence of antheridial cells attached to the resting spores. Species of these two genera have repeatedly been reported as occurring simultaneously in the cells of various hosts, although there is no record of the individual species, in such cases, having been isolated in pure cultures. In swollen filaments of *Achlya flagellata* which appeared to be infected with several species, the author (1939) immediately recognized *P. Saprolegniae* and *P. fusiforme*. In addition spherical, thick-walled resting spores, similar to the type described by Butler (1907) for certain *Pseudolpidium* species, were observed with occasional *Olpidiopsis* resting spores. It was found at once, however, that the spiny bodies which Fischer described as resting spores are nothing more than thin-walled zoosporangia which liberate zoospores directly without becoming dormant. It was thus obvious that Fischer's genus *Pseudolpidium*, based on the misinterpretation of these sporangia, is no longer valid. This viewpoint has been confirmed by the subsequent discovery of similar spiny sporangia in *O. vexans*, *O. fusiformis*, *O. varians*, and *O. Saprolegniae* by Shanor (1939).

When monospore cultures were established, the author (1939) found, however, that he was not dealing with several organisms but with a single species which produces smooth and spiny zoosporangia and forms thick-walled resting spores with or without attached antheridial cells. This discovery immediately raised the question whether or not any generic distinction can be made on the basis of this character of the resting spore. Pending further investigation of the nature of sex in this group, however, the author (1939) suggested that the genus *Pseudolpidium*, amended in accordance with the new facts, might be maintained for the asexual species described by Butler (1907), and that the organism with which we are dealing might be regarded tentatively as a *Pseudolpidium* species which, although predominantly asexual, may display some sexuality.

Since that time a thorough investigation of the variations in structure and sexual expression displayed by this new species has been made in an effort to establish its proper relationships and to evaluate some of the characters upon which generic and specific distinctions have been made in the past. Some of the results of this study are recorded in this paper.

MATERIALS AND METHODS

The technic employed in securing and maintaining the parasite is an adaptation of the method reported by Miss Berdan (1939). A pure stock culture of *Achlya flagellata* was maintained on Difco potato dextrose agar, while the parasitized host cultures were grown on sterile hemp seeds in sterile charcoal water. Transfer and renewal cultures were prepared by placing an infected "seed culture" in fresh charcoal water with a fresh *Achlya* culture. By repeated washing of the "seed culture" with sterile distilled water from a pressure wash bottle, protozoa were eliminated, and bacterial contamination was reduced to a minimum. It was found convenient to hold the culture in the depression of a moist chamber slide and to use a small aquarium pump to develop pressure sufficient to thoroughly clean the culture. Temperatures higher than approximately 25° C. were unfavorable, since they induced dormancy of the sporangia. This dormancy, however, could be broken by subjecting the culture to a temperature of about 15° C. for 24 hours.

Monosporangial cultures were prepared by collecting a few zoospores in a micropipette as they emerged from the sporangium and placing them in sterile charcoal water containing a pure culture of *Achlya* growing on a small block of agar. After a period of 24 hours, isolated sporangia appeared in the *Achlya* filaments, and with the aid of a low power dissecting microscope the parasitized filaments were separated without disturbing the sporangia. Filaments with single sporangia were then transferred to a culture dish containing pure *Achlya*, and in this way monosporangial infections were secured.

Similarly monospore cultures were obtained by collecting with a micropipette a drop of water containing several zoospores. The water was then spaced out in tiny droplets on a glass slide, and those containing a single zoospore were picked up again in sterile micropipettes and added to pure *Achlya* cultures.

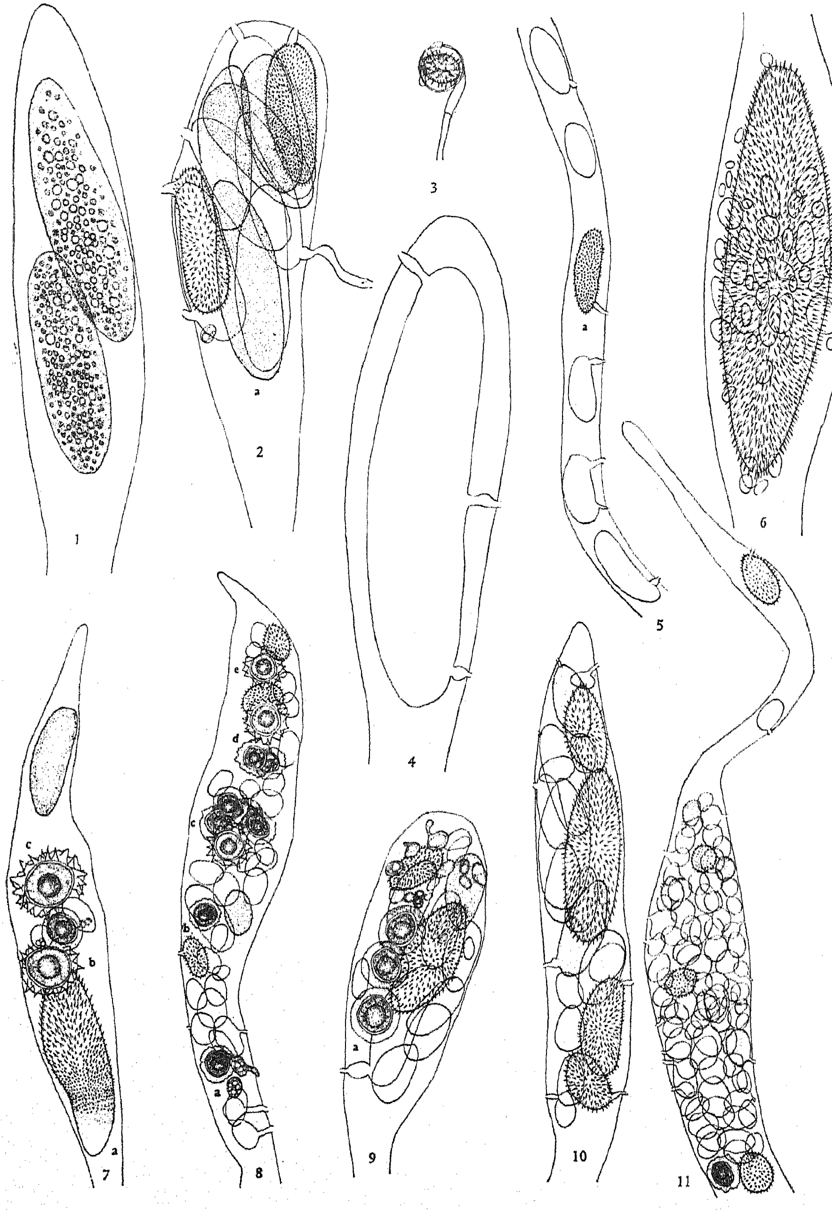
The infection and subsequent progressive stages in the development of the sporangia and resting spores of the parasite were observed in hanging drop cultures. When a small culture of *Achlya*, which had been allowed to remain for a few moments in water containing numerous zoospores, was lifted in a large pipette and placed on a cover-slip, the filaments spread out and clung close to the surface in a thin film of water, thus making it possible to use the oil immersion lens for observations. For the study of the developing zoosporangia, agar block cultures were used, because where the host presumably has a limited supply of food the thalli develop and mature rapidly without the interjection of long rest periods. For the study of resting spore development, the host was grown on fragments of raw meat.

OBSERVATIONS

Variations in Size, Shape, and Echinulation of the Zoosporangia. All monospore infections of *Achlya* so far observed have always resulted in the formation within the host filament of large, solitary, thin-walled zoosporangia (fig. 4). At maturity such solitary sporangia liberate large numbers of zoospores which re-infect the tips of young *Achlya* filaments. From such a secondary, multiple infection all the types of sporangia illustrated in figures 1–11 may result.

Correlations between the size of the sporangia, the size of the localized swellings of the host hyphae, and the number of sporangia in each swelling were sought. In this connection, however, we are dealing with large, aseptate filaments in which it is difficult to determine the unit of host protoplasm involved. The vigor of the host filaments and the volume of protoplasm which they might contain, moreover, vary so greatly that the interpretation of sporangial variation in terms of population counts and measurements proved impractical. It was soon found better to rely upon observational methods.

In hanging drop cultures it was possible to determine the approximate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numbers of zoospores infecting various filaments and to determine also the time at which certain infections took place relative to other local infections. As described above, solitary infections give rise to solitary sporangia which may become very large (fig. 4) if the host filament contains copious amounts of protoplasm but which will mature quickly without attaining great size if the supply of host protoplasm is limited. When two or several zoospores penetrated a filament more or less simultaneously, smaller sporangia of somewhat uniform size developed (figs. 1, 2). The size of the sporangia decreases as the number in the filament increases.

In not too congested filaments the sporangia attain appreciable size and assume a more or less ellipsoidal shape. When filaments were beset by large numbers of spores, however, large swellings, filled with small, spherical or oval sporangia measuring 11.5–50 microns in their largest diameter, were formed (fig. 11). It was also observed that when multiple infection of a filament which already contained one or several developing thalli occurred, the numerous sporangia formed were dwarfed (fig. 6). Apparently in such cases the older thalli absorb the bulk of the food and consequently deprive the younger thalli of adequate nourishment.

The ornamentation of the walls of zoosporangia varies from very fine echinulations (fig. 2a) to large heavy bristles (fig. 6). Attempts were made to correlate the production of bristles with the age of the culture, the vigor of the host, and other general environmental factors. No such correlations could be established, however, since it was found that smooth and rough-walled sporangia were produced simultaneously side by side (figs. 2, 10), and the entire range of variation from smooth to extremely rough walls was often observed on a single sporangium (fig. 7a).

The progressive stages of bristle formation were often observed in hang-

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Explanation of figures 1–11

FIG. 1. Two elongate thalli of *O. Achlyae* in a swollen tip of an *Achlya* filament. ×93. FIG. 2. Several smooth and rough-walled empty zoosporangia of approximately equal size in a swollen filament. ×93. FIG. 3. A small, spiny zoosporangium in an *Achlya* oogonial cell. ×93. FIG. 4. A large solitary zoosporangium, with three exit tubes, in a swollen *Achlya* filament. ×93. FIG. 5. Several small, empty, smooth and rough-walled zoosporangia which have matured in a filament without causing any appreciable swelling of the host cell. ×93. FIG. 6. A single large, spiny zoosporangium in a swollen filament with numerous smaller, smooth sporangia. ×93. FIG. 7. A swollen *Achlya* filament containing a parthenogenetic resting spore of *O. Achlyae*, two sexual resting spores *b* and *c* and two rough-walled sporangia; sporangium *a* is smooth at one end and heavily bristled at the other. ×93. FIG. 8. A swollen *Achlya* filament with numerous, small, smooth and rough-walled zoosporangia and asexual (*a–d*) and sexual (*e*) resting spores. ×93. FIG. 9. Large and small, smooth and rough-walled zoosporangia with three smooth-walled resting spores (*a*). ×93. FIG. 10. Oval to elongate, smooth and rough-walled zoosporangia in a slightly swollen filament. ×93. FIG. 11. Numerous spherical to oval, smooth and rough-walled zoosporangia in a swollen *Achlya* filament; two isolated thalli have caused little swelling of the host filament in their vicinity. ×93.

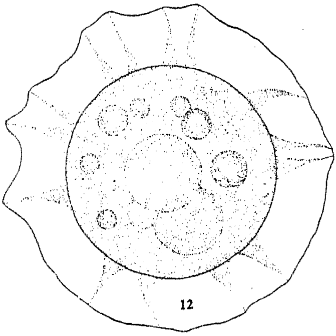
ing drop cultures. On the surface of sporangia which had attained approximately their mature size but were still surrounded by an appreciable amount of visible host protoplasm, small, hyaline, indefinite bristles were sometimes discernible. Such bristles increase in number, size, and density until, at maturity, the sporangium may appear similar to that shown in figure 6. As this development takes place the visible host protoplasm gradually diminishes until, at maturity, the sporangium is suspended in a hyaline medium. Although it has not been conclusively demonstrated that these bristles arise by a localized deposition of host protoplasm, this is suggested by the fact that they develop as the refractive material about them diminishes. This is in agreement with the observations of Fischer (1882). Furthermore, when such rough-walled sporangia are treated with zinc chloro-iodide, the wall stains blue, but the bristles give no cellulose reaction. The actual chemical nature of the bristles, however, remains unknown.

These observations on living zoosporongia seem to indicate that variations in their size are dependent upon the vigor of the host, the number of thalli developing in a given locality, and, within a single filament, the time of penetration relative to other local infections. They vary, accordingly, from large, solitary, cylindrical sporangia to small, spherical ones which develop in congested filaments. Although the factors controlling the formation of bristles are obscure, they appear to arise by a direct, localized deposition of host protoplasm upon the surface of the thalli.

Development and Variations of the Exospore. The great variability which characterizes the exospore, in this species is of particular interest in view of the great stress which has been placed upon this structure in the determination of species of *Pseudolpidium* and *Olpidiopsis.*

Explanation of figures 12–26

FIG. 12. Origin of spines of the exospore within the hyaline layer drawn from living material. × 580. FIGS. 13–15. Successive stages in the development of a thin, warty exospore on a resting spore which absorbed most of the host protoplasm during its early developmental stages. × 470. FIG. 16. An empty male cell attached to two mature resting spores. × 470. FIG. 17. A mature sexual resting spore with three empty male cells attached; margin of the homogeneous layer is visible about the apices of the spines. × 470. FIG. 18. A mature resting spore with two attached male cells which still contain their contents. × 470. FIG. 19. Cytoplasmic strands running from the apices of the broad-based spines of an asexual resting spore. × 470. FIG. 20. A developing resting spore stained with haematoxylin showing origin of spines within the homogeneous layer by centripetal condensation of protoplasm along definite lines. × 580. FIG. 21. A parthenogenetic resting spore bearing long, narrow spines. × 580. FIG. 22. A mature resting spore with an exospore which is part smooth and part spiny. × 580. FIG. 23. A mature asexual resting spore of *O. Achlyae* possessing an undulant exospore. × 580. FIG. 24. A mature resting spore bearing a halo of hair-like spines. × 580. FIG. 25. A mature resting spore of *O. Achlyae* illustrating how the development of the exospore has conformed with the wall of the host filament—i.e., with the distribution of the host protoplasm. × 580. FIG. 26. Two sexual resting spores *A* and *B* with their associated male cells *X* and *Y* which have been enveloped by a common wall. × 580.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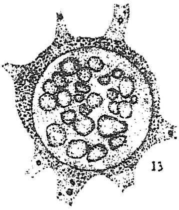
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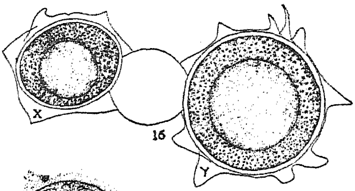

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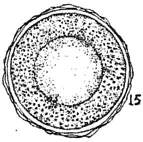
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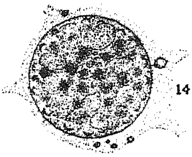
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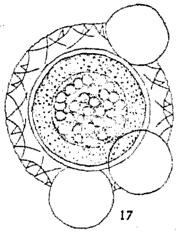
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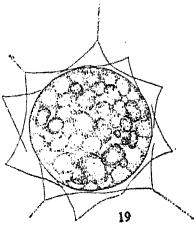
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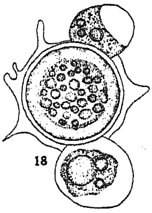
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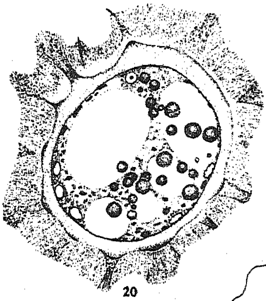
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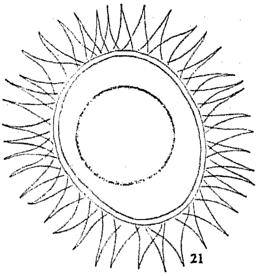
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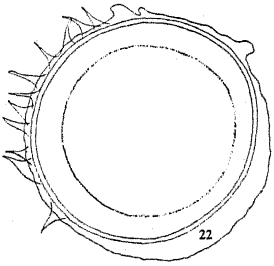
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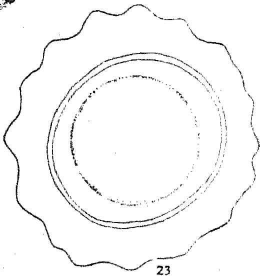
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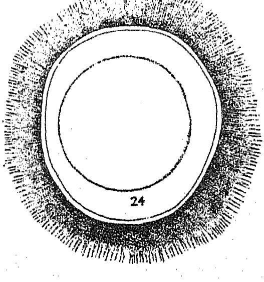
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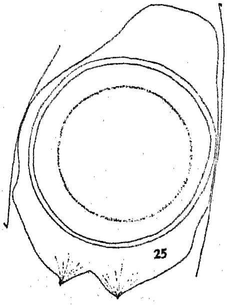
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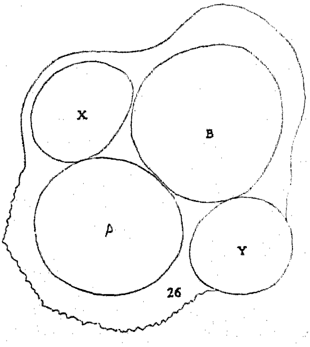

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Young developing resting spores in the living condition can be distinguished from incipient zoosporangial thalli at a fairly early stage by their more opaque protoplasmic content and, to some extent, by the noticeably thicker layer of granular, degenerating host protoplasm which usually surrounds the young resting spores. The exospore usually first becomes evident as a homogeneous, amorphous layer which develops centripetally around the thallus, gradually replacing entirely the mass of granular host protoplasm. At maturity, this layer may maintain a fairly even contour (fig. 23), although, in stained preparations, radially arranged lines, which appear to be regions of condensation, may be observed extending inward from the outer margin of the exospore. In most cases, however, this homogeneous layer becomes organized, to a greater or lesser degree, into spines of various sorts (figs. 17, 21, 22, 24). Such spines, the beginnings of which can often be observed in living material as slightly more opaque, conical regions (fig. 12), are elaborated within the confines of the homogeneous layer, the outer margin of which often remains visible for some time (fig. 17). A resting spore, fixed and stained in a stage of development comparable to that shown in figure 12, is illustrated in figure 20. A tendency for the lines of deposition to become somewhat localized and organized into conical "bundles," which seem to represent incipient spines, is striking. It is to be further noted that the lines of deposition do not extend all the way in but appear to be developing from the outer margin of the layer toward the centre. This observation is in agreement with that of Butler (1907) on *Pseudolpidium Pythii*, for which he describes the spines of the resting spores as arising within a light band "by condensation of protoplasm along definite lines" centripetally.

On a few spores spines have been seen to arise apparently by direct deposition of host protoplasm without the formation of a homogeneous layer. Cytoplasmic strands were usually observed to radiate from the tips of such spines as were newly formed (fig. 19).

Like the bristles of the zoosporangia, the exospores fail to react with zinc chloro-iodide, in contrast to the endospore which gives a brilliant cellulose test. Attempts to demonstrate the actual chemical composition of the exospore have been unsuccessful. It can be definitely said, however, that its deposition is intimately associated with the layer of host protoplasm directly impinging upon the thallus. Figure 25 illustrates a spore the formation of whose exospore has apparently been governed by the limitations of the wall of the host filament—i. e., by the distribution of the host protoplasm. The homogeneous layer seems to result from a direct deposition of host protoplasm, and the organization of spines seems to be accomplished by a regional condensation and deposition of this substance along more or less radial lines.

Strong evidence in support of this interpretation is the very poor development of exospores by resting spore thalli which use up most of the host protoplasm in their early developmental stages (figs. 13–15). Such spores, at maturity, may be enclosed by a very thin, warty exospore; the outer wall of some that were observed was almost entirely lacking. It might be argued that the host protoplasm is first absorbed by the thallus and later the exospore is secreted. In this case, accordingly, it would be assumed that most of the food material was needed by the maturing thallus and that little excess was left available for wall secretion. The deposition of the exospore begins fairly early, however, and despite its increasing thickness the host protoplasm steadily diminishes. The homogeneous layer might be confused, in certain respects, with the digestion cavity which often surrounds intracellular parasites. Incipient resting spores which have been dissected out at this stage, however, have been found to be enclosed in a definite, structural layer which does not appear to be a region of digestion or absorption. Judging from the difficulties encountered in bringing about penetration of mature spores by fixatives and intra-vitam stains, it seems improbable that much absorption by the thallus would go on after the formation of the exospore has begun. Consequently, the gradual disappearance of the host protoplasm which takes place as the exospore layer increases in thickness is best explained by assuming direct deposition of host protoplasm upon the surface of the thallus. Figure 26, drawn from sectioned and stained material, shows two resting spores A and B, with their related male cells, X and Y respectively. It is to be noted that their exospores are completely confluent and that male cell X is entirely surrounded and embedded. Such a condition seems to suggest exospore production by deposition and direct transformation of host protoplasm rather than separate secretion by each individual thallus.

A consideration of the various configurations which the exospores of mature resting spores of this species may assume is interesting and suggestive of the synonymy which might arise by attributing false significance to these variations. Mature resting spores of our species are often invested by a dense layer of broad based spines similar to those described for *O. fusiformis* and *O. minor* (fig. 17). Sawada (Tokunaga 1933) in 1912 described a species, *P. stellatum*, solely upon the basis of the resting spores observed. These spores, which he describes as similar to those of *O. minor* but lacking attached male cells, are simulated by asexual spores of our species. Long, tapering spines (fig. 21) similar to those described for *O. Saprolegniae* have also been observed, while undulating exospores like those described for *O. major* and *P. incrassata* are not uncommon in cultures of the species here considered (fig. 23). Spores surrounded by a halo of hair-like spines or fibrillae simulating the spores described by De Wildeman (1895) for *O. fibrillosa* regularly occur (fig. 24), while resting spores which have developed under conditions providing a minimum of nourishment often possess, at maturity, a thin, warty exospore similar to that described by Barrett (1912) for *O. vexans* (fig. 15). In addition, many other irregular variations of the exospore are commonly encountered in cultures of this species (figs. 16, 18, 22, 25).

It is not maintained that all the species whose resting spores are simulated by this one extremely variable organism are necessarily invalid. Nevertheless, the apparent method of formation of the exospore and the infinite variation which it may exhibit within one species indicate that it is not an infallible diagnostic character upon which to base generic distinctions. When all species concerned have been re-collected and critically studied in pure culture, we may learn that many of them are synonymous while others, which may be confined to various definite hosts, may prove to be physiological strains of a few distinct species.

Sex Determination. When Cornu (1872) observed small, empty thalli attached to larger resting spore thalli he assumed that the smaller cells were antheridia. His belief was confirmed in 1878 when Reinsch observed the movement of the contents of the smaller into the larger thallus. Since that time this interpretation has been generally accepted and the terms "antheridium" and "oogonium" have been applied to the smaller and larger thalli, respectively, and the fusion of these cells has been referred to as being a primitive type of oomycetous reproduction. Scherrfel (1925) looks upon the resting spores of *Olpidiopsis* as oospores without periplasm and, upon this basis, he outlines a possible origin of the *Pythium*-Peronosporaceae group from simpler species through *Olpidiopsis*. No investigation of sex determination in these species has ever been attempted, however, and the actual origins of the so-called antheridial and oogonial thalli remain obscure. Barrett (1912) states that when these thalli first become recognizable it is impossible to say whether they have had separate origins or whether they have been derived by an unequal division of a single thallus. He believes, none the less, with all other investigators of *Olpidiopsis* species, that resting spore formation invariably involves fusions of cells. The spores of the species under consideration, however, may be formed with or without fusions while the ratio of so-called sexual to asexual spores may show noticeable variation.

From a series of counts made on resting spores of various culture generations, it was found that only one quarter of the resting spores of our species have attached antheridial cells. It has been noted, however, that the ratio of sexual to asexual spores in consecutive culture generations may show variation which cannot be correlated with any easily recognizable environmental factor. When studying pure cultures of this species it is not unusual to find certain cultures which exhibit no sexuality whatever, while others, growing under the same conditions, display only resting spores of the *Olpidiopsis* type. It has been observed by Barrett (1912), the author, and others that resting spores are more abundant in cultures grown in stale water, while Diehl (1935) points out that low temperatures have a similar effect. Observations on this species, moreover, have shown that lower temperatures not only stimulate resting spore formation but, in cultures maintained at low temperatures, although the sexual-asexual ratio may still vary, the percentage of sexual resting spores is usually markedly higher.

In several cases, similar to that illustrated in figure 16, male cells attached to two female thalli have been observed. In the thalli illustrated the contents of the male cell passed into the smaller of the two female thalli although the larger thallus matured quite as readily as did the smaller "fertilized" thallus. The passage of only a part of the contents of the male cells into the larger thalli in the "fertilization" process has often been observed, while the total failure of attached male cells to function frequently occurs (fig. 18). It is evident that fusion is not essential to resting spore formation and that male cells, even when present, do not always participate in the maturation of the female thallus.

It has been mentioned by Shanor (1939) that, during his investigation of *O. luxurians*, spores were observed which appeared to be formed asexually, but upon closer observation these proved to be merely "inadvantageously orientated" sexual spores, the male cells of which were hidden from view. That this is not true of the "parthenogenetic" resting spores of our species has been repeatedly shown by dissecting the spores out in glycerine where they could be rolled over and over for examination from all sides.

At the outset it was postulated that the production of sexual and asexual spores by this extremely variable species might be explained on the basis of heterothallism. It was found by the author (1939), however, that heterothallism does not exist in this species, inasmuch as sexual spores occur in cultures which have been propagated from a single zoospore. Moreover, if we are to assume genotypic differentiation of sex in this species, there are basic assumptions to be made which, in themselves, seem to totally discredit any claim of sex segregation. In the case of monospore cultures exhibiting sexuality it would be necessary to assume that the single zoospore from which the culture was propagated was diploid with factors for maleness and femaleness. In the maturation of the primary sporangium formed by the single spore we must further assume that zoospores similar to the original were formed by mitosis, while in other parts of the same sporangium meiosis occurred in the production of genotypically differentiated male and female gametes. These in turn would give rise to the zoosporangial "antheridial" and "oogonial" thalli which appear in the secondary infection. In all the prepared, zoosporangial material studied to date, however, no indication of meiosis has been found to support this assumption which, in itself, seems improbable enough to discredit the entire hypothesis.

It has been stated above that low temperatures appear to increase the percentage of sexually formed resting spores, while the ratio of sexual to asexual resting spores varies constantly without any apparent relation to environmental factors. As will be more clearly brought out in a following paper, the male and female thalli of this species have been found to be multinucleate and essentially similar to the zoosporangial thalli. The mature resting spores are likewise multinucleate, and upon germination they function as sporangia, liberating zoospores through an exit tube. In this regard these resting spores differ from the uninucleate resting spores which Hillegas (1940) has observed for *Endochytrium operculatum*, which germinate indirectly by producing an evanescent zoosporangium in which nuclear divisions take place prior to the delimitation of zoospores. It seems, at least in the species which we are considering, that all incipient zoosporangial thalli are potential male and female cells which, under certain conditions, become somewhat differentiated and function in the formation of resting spores. The use of the terms ''antheridium'' and ''oogonium'' to denote the smaller and larger fusion thalli, respectively, is unfortunate and misleading. These terms, in their proper sense, refer to gametangia producing male and female gametes. Consequently, these thalli, when they fuse, may more properly be referred to as male and female thalli.

All our observations indicate that this species is haplosynoecious and that sex is phenotypically determined. Upon the basis of such a hypothesis the wide range of variation in sexual expression and the ability of certain environmental factors to influence such variation can, to some extent, be explained. Conclusive evidence of the truth of the hypothesis, however, must await the results of much more experimentation and cytological demonstration of meiosis occurring in the germination of the resting spores.

DISCUSSION

The foregoing observations on resting spore formation in the species with which we are dealing show conclusively that distinctions drawn between sexual and asexual species are totally unwarranted. The formation of resting spores of the *Olpidiopsis* type does not involve fusions between genotypically differentiated gametes but apparently merely represents a reaction between incipient zoosporangia which, under certain conditions, may become somewhat modified to function in resting spore formation. It has been demonstrated, moreover, that such fusions are in no way essential to resting spore development and that, in this particular species, the percentage of sexual spores formed may vary over a wide range in accordance with the temperature and other obscure external factors. Consequently, it is obvious that *Pseudolpidium* should be merged with *Olpidiopsis* and that the description of the latter genus should be amended to include species with smooth and

spiny zoosporangia which may form either sexual or asexual resting spores. The author is accordingly revising the generic diagnosis as follows:

OLPIDIOPSIS Cornu, Ann. Sci. Nat. V, **15**: 114. 1872. *Pleocystidium* Fisch, Sitz.-ber. Phys. Med. Soc. Erlangen **16**: 29–66. 1884. *Diplophysa* Schroeter in Cohn's Kryptog. Fl. Schlesiens **3**: 175–197. 1889. *Olpidiopsis* (Cornu) Fischer, Rabenhorst Kryptog. Fl. **1**^{4}: 37. 1892. *Pseudolpidium* Fischer in Rabenhorst Kryptog. Fl. **1**^{4}: 33. 1892. *Pseudolpidiopsis* Minden. Krypt. Fl. Mark Brandenburg **5**: 209–422. 1911.

Thallo intramatricali, monocentrico, holcarpico, primum nudiusculo (ut videtur) sed protoplasma hospitis inmixto, maturitate distincto pariete cellulosam habente disiuncto. Zoosporangiis solitariis vel numerosis, hyalinis vel parce granulosis, levibus vel echinulatis, globosis, ovalibus-ellipsoideis, cylindriceis, sacculatis vel irregularibus, cum una aut amplius tubulis exeuntibus, latis, acutis vel cylindriceis, rectis, curvis spiriformibus, brevibus vel elongatis, quae usque ad parietem matricis pertinere aut etiam se extra proicere solent. Zoosporis hyalinis, minutissime granulatis, interdum cum gutta contrahende, ovali, ellipsoideo, vel aliqua ex parte elongata atque reniformi; hetero- et isoconti flagellis a latere prope anteriorem partem insertis, flagello breviore protinus, longiore retro plerumque derecto; maturis emergentibus subitoque enatantibus vel interdum quiete cumulo ostio tubulae aliquamdiu manentibus; aequaliter haud emicatim movent ex occasione flagellatis retractis tranquilliter quiescentes. Sporis perdurantibus, gamicis, agamicis vel parthenogeneticis, ovalibus ellipsoideisve, hyalinis, brunneis, levibus, verruciformibus, undulatis, echinulatis, unum aut amplius globulos refringentes magnos parvosve aut habentibus aut carentibus; antheridia, cum adsunt, solitaria vel numerosa, hyalina, levia, spiniformia vel echinulata. Germinatio directa, tubula exeunte formata et biflagellatis zoosporis liberatis.

Thallus intramatrical, monocentric, holocarpic, appearing more or less naked but immiscible with the host protoplasm when young, becoming invested with a definite cellulose wall at maturity. Zoosporangia solitary or numerous, hyaline or slightly granular, smooth or spiny, spherical, oval, ellipsoidal, elongate, sac-like or irregular with one or several broad, tapering or cylindrical, straight, curved, coiled, short or elongate exit tubes which may end flush with the surface of the host cell or may project beyond it. Zoospores hyaline with numerous minute granules, and occasionally a contractile vacuole, oval, ellipsoidal, or somewhat elongate and reniform, hetero- and isocont; flagella inserted laterally near the anterior end, the shorter one usually directed forward and the longer backward; emerging fully formed and swimming directly away or occasionally lying quiescent in a mass for a moment at the mouth of the exit tube; movement even, not darting, interrupted by one or several rest periods during which the flagella may be retracted. Resting spores sexual and asexual or parthenogenetic, oval or ellipsoidal, hyaline, brown, smooth, warty, undulating or wavy, spiny, with or without one or several large or small refringent globules; male cells, when present, single or numerous, hyaline, spherical, smooth, warty or spiny. Germination of the resting spore direct by formation of an exit tube and liberation of biflagellate zoospores.

Few of the species of *Pseudolpidium* and *Olpidiopsis* which have been described have been adequately studied and we have very little accurate knowledge of their variability and host relationships. Yet it is primarily upon the basis of the host range and exospore variations that these species have been determined. It has been pointed out above that the resting spores of several species which are now considered as distinct are simulated in monospore cultures of the extremely variable species which we are considering. In view of this, it does not appear that the character of the exospore is a suitable, fundamental diagnostic character. It seems highly probable that many of the species which have been described may prove to be synonymous with or nothing more than physiological strains of a few legitimate species. This new species, likewise, may be synonymous with several others which are at present considered distinct but, until all these related species have been critically studied in monospore cultures, the exact identity and relationships of this species must remain in doubt. For this reason I am provisionally naming the species until the genus as a whole is better known.

Olpidiopsis Achlyae McLarty sp. nov. (ad int.). Zoösporangiis solitariis vel numerosis, plerumque in matricis cellibus turgidis terminalibus vel intercalaribus positis; brunneolis, parce granulatis, maturitate pariete cellulosam habente circumvallatis, levibus vel spinis angustis vel crassis quae cellulosa carent; sphaericis, ovalibus, ellipsoideis vel elongatis, magnitudine variis, 13.2–112.4 μ diametro × 115.0–666.4 μ; tubulis exeuntibus (1–3 numero) quae saepissime extra superficiem hospitis longe pertinent. Zoosporis hyalinis minutissime granulatis, ovalibus, sphaericis, vel parce reniformibus, 3.2–5.7 μ × 2.9–4.3 μ, plerumque c. 3.1 × 4.2 μ, cum duobus subaequalibus flagellis a latere prope anteriorem partem coniunctis. Sporis perdurantibus gamicis, agamicis, vel parthenogeneticis, sphaericis vel ovalibus, 22.8–122.4 μ (plerumque c. 50.0 × 41.0 μ), brunneis, cum uno (compluribus rarius) permagno globulo refringente. Endosporio cellulosam habente, levi, 1.0–1.5 μ diametro. Episporio cellulosa carente, 1.0–11.4 μ, spinis verruciformibus, parvis vel magnis, basi angusto vel lato, fibrillis capilliformibus vel cum margine levi, undulato vel paullum serrato. Antheridia, cum adsunt, contenta in oogonium interdum (non tamen semper) ejiciunt forma zoosporangiis similia, 1–3 uni oogonio adiunctis, sphaericis, vel ovalibus, tenui pariete, levibus, interdum in episporio conclusa. Spora perdurans germinatione in sporangium transformatur, zoosporis tubula exeunte liberatis.

Zoosporangia solitary or numerous, usually localized in a terminal or intercalary swelling of the host filament, slightly brown and granular, enclosed at maturity by a cellulose wall, smooth or covered with fine or coarse non-cellulose bristles; spherical, oval, ellipsoidal or elongate, variable in size, 13.2–112.4 μ diam. × 115.0–666.4 μ; one to three exit tubes which may extend considerably beyond the surface of the host filament. Zoospores hyaline with numerous small granules, oval, spherical, or somewhat reniform, 2.3–5.7 μ × 2.9–4.3 μ, usually about 4.2 × 3.1 μ, with two approximately equal flagella attached laterally near the anterior end. Resting spores sexual and asexual or parthenogenetic, spherical or oval, 22.8–122.4 μ (usually about 50.0 × 41.0 μ), brown, with several or commonly one, large refringent globule.

Endospore composed of cellulose, smooth, 1.0–1.5 μ in thickness. Exospore not composed of cellulose, varying from 1.0–11.4 μ in thickness, with warty protuberances, small or large, narrow or broad-based spines, hair-like fibrillae or with an entire, undulant or slightly serrate margin. Male cells, when present, may or may not discharge contents into female thallus, similar in appearance to zoosporangia, one to three attached to one female thallus, spherical or oval, thin-walled, smooth, sometimes embedded in the exospore. Resting spore in germination transformed into a sporangium liberating zoospores by means of an exit tube.

Parasitic in *Achlya flagellata* Coker from a pool on the campus of the University of Western Ontario, London, Canada, September 1937.

It has been shown by the author (1939) that the spiny bodies which Fischer described as resting spores of *Pseudolpidium Saprolegniae* and *P. fusiforme* are merely rough walled zoosporangia and that, inasmuch as they all occur in monospore cultures of *O. Achlyae,* the sporangial types which Fischer regarded as diagnostic of his two species cannot be regarded as being limited to any one organism. This viewpoint has been confirmed by the subsequent observations of Shanor (1939). Consequently, *P. Saprolegniae* must be recombined with *O. Saprolegniae* while *P. fusiforme* and *O. minor* must be recombined under the original name, *O. fusiformis,* as Shanor has already suggested. *Pseudolpidium stellatum* was described by Sawada in 1912 (Tokunaga 1933) when he observed resting spores, similar to those of *O. minor* but without adjacent cells, occurring frequently in association with *P. fusiforme.* In view of our observations on *O. Achlyae* it seems advisable to combine this species also with *O. fusiformis* and to consider the latter as a sexual-asexual species.

Olpidiopsis Aphanomycis was originally described by Cornu (1872) and included as a member of the genus although he did not observe resting spores. Consequently Fischer (1892) transferred this species to *Pseudolpidium* as *P. Aphanomycis.* Dangeard (1891) illustrated a resting spore of *O. Aphanomycis* with no adjacent cell. Butler considered this to be the true resting spore of *P. Aphanomycis.* Subsequently, Petersen (1910) described sexual resting spores for *O. Aphanomycis* and commented on the similarity between this species and *O. Saprolegniae.* Barrett (1912) described another species, *O. luxurians,* occurring in filaments of *Aphanomyces.* Shanor (1939) has discussed the similarities which exist between all of these parasites of *Aphanomyces* which have been reported by Cornu (1872), Dangeard (1891), Butler (1907), Petersen (1910), and Barrett (1912) and suggests that later investigations may prove that they are all synonymous with Cornu's original species. This may be true, but at the present time it seems advisable to maintain Barrett's species and to combine the remainder of the sexual and asexual parasites of *Aphanomyces* which have been described under Cornu's original name *O. Aphanomycis.*

Only one of the resting spores which Cornu (1872) illustrated for *O. incrassata* possessed an antheridial cell. Consequently Fischer (1892) tentatively transferred the species to *Pseudolpidium* as *P. incrassata*. Since that time Sparrow (1933) has reported *P. incrassata*, while Petersen (1910) considers this species as synonymous with *P. Saprolegniae*. Maurizio (1895) claims that the resting spores of *O. incrassata* are identical with those of *O. major*. It appears that Cornu (1872), Maurizio (1895), and Sparrow (1933) were dealing with the same organism. Accordingly the author proposes to combine *P. incrassata* and *O. major*, which has not been observed since its description, under Cornu's original name, *O. incrassata*, and to consider the species as one which produces sexual and asexual resting spores.

Pseudolpidium Pythii and *P. gracile*, as described by Butler (1907), possess relatively thin-walled resting spores covered with fine spines. Very little is known of these species, although each has been observed since Butler's time. The resting spores of these species, as they are illustrated in the literature, appear very similar in appearance to spiny zoosporangia. Until they are re-collected and critically examined, these species may be transferred to *Olpidiopsis* as strictly asexual species.

Pseudolpidium glenodinianum and *P. Sphaeritae* (Fischer 1892) and *P. deformans* (Serbinow 1907), of which no resting spores are known, may be transferred to the genus *Olpidiopsis* on the basis of their biflagellate zoospores and maintained as very doubtful species until their real identity can be demonstrated.

SUMMARY

A new species, *Olpidiopsis Achlyae*, which produces smooth and spiny-walled zoosporangia and sexual and asexual resting spores, has been described. The genus *Pseudolpidium* has been merged with *Olpidiopsis* and the diagnosis of the latter has been revised accordingly.

Variations in the size and shape of the zoosporangia seem to depend directly upon the amount of nourishment available to the developing thalli. Non-cellulose bristles appear to be formed by a localized deposition of host protoplasm upon the surface of the incipient zoosporangium.

Evidence has been presented in support of the view that the exospore, which, in contrast to the endospore, is not composed of cellulose, is formed by a localized deposition of host protoplasm upon the surface of the parasite.

Resting spores, which have been described as characteristic of several species of *Olpidiopsis*, are commonly simulated in pure cultures of *O. Achlyae*. The marked variability of the exospore in this species indicates that it is not a suitable diagnostic character upon which to base specific distinctions.

Fusions between thalli are in no way essential to the formation of resting spores by this species. *O. Achlyae* is, apparently, haplosynoecious, and sex, when present, is phenotypically determined.

This study of pure cultures of *O. Achlyae* clearly indicates the need for a critical re-examination of all species of *Olpidiopsis,* which, for the most part, have been very inadequately studied.

The writer wishes to express his appreciation and thanks to Prof. John S. Karling, under whose direction this investigation has been carried on, for his generous assistance and stimulating criticism; to Prof. Helen Berdan, who provided the original cultures from which this species was isolated; and to Prof. J. N. Couch for the identification of the species of *Achlya.* Courtesies extended by the writer's colleagues on the Botany faculty of Dartmouth College have greatly facilitated the completion of this study.

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NEW OR NOTEWORTHY SOUTH AMERICAN ERIOCAULACEAE

HAROLD N. MOLDENKE

Recent collections of South American plants sent to the writer for determination have brought to light a number of hitherto undescribed species and varieties in the *Eriocaulaceae* and have revealed the desirability of reducing a specific combination to varietal rank.

Paepalanthus Archeri Moldenke, sp. nov. Herba acaulis nana; foliis caespitosis recurvatis linearibus, ad basim densissime longeque villosis, ad apicem utrinque glabratis; pedunculis stramineis 3-costatis densiuscule longeque pubescentibus; vaginis subglabratis, ad apicem oblique lobatis.

Dwarf stemless herb; leaves tufted, recurved, appressed to the ground, olivaceous, linear, 4–10 mm. long, 0.5–1 mm. wide at the middle, blunt at apex, not fenestrate, very densely long-villous with silky-white hairs at the base, glabrous on both surfaces at apex, the basal villosity forming a very dense and conspicuous white cottony tuft or cushion at the base of the plant; peduncles stramineous, very slender, 3–4.5 cm. long, twisted, 3-costate, rather densely long-pubescent with divergent whitish gland-tipped hairs; sheaths closely appressed to the peduncles, about 1 cm. long, twisted, many-costate, subglabrate except for the long-ciliate obliquely lobed mouth, the lobe 2–3 mm. long, acuminate and somewhat recurved at apex; heads hemispheric, about 3 mm. high and 6 mm. in diameter, densely many-flowered; involucral bractlets numerous, many-seriate, chestnut-brown (the inner ones lighter), obovate or spatulate, 1.9–2.5 mm. long, 0.9–1.4 mm. wide, rounded at apex, glabrous on both surfaces; receptacle very densely long-villous with white hair; receptacular bractlets hyaline, obovate, about 3 mm. long and 1.2 mm. wide, rounded at apex, long-cuneate at base, appressed-pilose on the back; staminate florets: long-pedicellate; sepals 3, connate at the base only, hyaline, obovate-elliptic, about 1.9 mm. long and 0.7 mm. wide, rounded at apex, densely appressed-villous on the back toward the apex; petals connate into a hyaline, hollow, glabrous, minutely 3-lobed, eglandular tube; stamens 3, less than 1 mm. long, white; pistillate florets: short-pedicellate or subsessile; sepals 3, connate at base, hyaline, about 1.2 mm. long and 0.3 mm. wide, obovate, rounded at apex, densely pilose on the back toward the apex; petals 3, separate, minute, orbicular, about 0.3 mm. long and wide, glabrous, eglandular; pistil about 0.7 mm. long; styles, stigmas, and style-appendages 3 each, white.

BRAZIL—MINAS GERAES: Serra do Cipó, alt. 1800 m., *William Andrew Archer 3677*, August 5, 1936, TYPE; in the United States National Herbarium at Washington.

Paepalanthus Killipii Moldenke, sp. nov. Herba perennis; caule elongato folioso stolonifero; foliis imbricatis graminoidiis subacutis integris utrinque sparse obscureque puberulentibus et plusminus albido-pilosis, glabrescentibus nitidis; vaginis adpressis sparse piloso-hirsutulis, ad apicem oblique lobatis; pedunculis tenuibus numerosis erectis stramineis 2-costatis glabris nitidis; capitulis cinereis.

Perennial herb; stem slender, elongate, to 17 or more cm. long, decumbent at base, erect at apex, leafy; abbreviated branches issuing from the stem near its base in stolon-like fashion, bearing diminutive young "plants" with very narrow leaves, 2 or 3 abbreviated peduncles, and tiny few-flowered heads; leaves (on normal plants) overlapping, grass-like, olivaceous, 3.5–7 cm. long, 1.5–7 mm. wide (usually 5–7 mm. wide), subacute at apex, entire, sparsely and obscurely puberulent on both surfaces, with scattered long and whitish pilose hairs interspersed, especially toward the base, glabrescent in age, shiny on both surfaces, not fenestrate, many-nerved; sheaths tubular, closely appressed to the peduncles, 3–5 cm. long (smaller on the basal stolons), sparsely pilose with long, scattered, weak, whitish, hirsutulous, spreading hairs, more densely so at the obliquely lobed mouth, the lobe 2.5–4 mm. long, attenuate at apex; peduncles slender, numerous, about 50 per plant (except on the basal stolons), erect, 9–27 cm. long, stramineous, 2-costate, glabrous and shiny throughout; heads hemispheric, ashy-gray, 3–6 mm. in diameter (much smaller on basal stolons); involucral and receptacular bractlets similar, oblong or obovate, dark-brown or blackish, about 1.2 mm. long and 0.7 mm. wide, rounded at apex, glabrous on both surfaces except for a tuft of short erect hairs at the apex; receptacle densely long-villous; staminate florets: short-pedicellate; sepals 3, very slightly connate only at the very base, dark-brown, obovate, about 1 mm. long and 0.7 mm. wide, rounded at apex, glabrous on both surfaces; petals connate into a hyaline, hollow, glabrous, eglandular, minutely 3-lobed tube; stamens 3, about 1.4 mm. long, white, glabrous; pistillate florets: very short-pedicellate; sepals 3, connate only at the very base, obovate, dark-brown toward apex, about 1.4 mm. long and 0.6 mm. wide, rounded at apex, appressed-villous on the back; petals 3, free, hyaline, narrowly oblanceolate, about 1.4 mm. long and 0.4 mm. wide, rounded at apex, densely long-villous; pistil about 1.4 mm. long, glabrous; styles, stigmas, and style-appendages 3 each, glabrous.

COLOMBIA—SANTANDER SUR: Eastern Cordillera, Mesa de los Santos, marshy land, alt. 1500 m., *Ellsworth Paine Killip & Albert Charles Smith 15,299*, between December 11 and 15, 1926, TYPE; in the United States National Herbarium at Washington. Named in honor of E. P. Killip.

Paepalanthus lodiculoides Moldenke, sp. nov. Herba perennis; caulis abbreviatis lignosis caespitosis densissime albo-villosis vel -tomentosis; foliis linearibus densissime imbricatis valde adpressis glabris; pedunculis gracillimis abbreviatis sparsissime pilosulis vel glabris; capitulis solitariis.

Perennial herb, very densely tufted; stems apparently much abbreviated and woody at base, 1 or 2 cm. long, very densely white-villous or -tomentose with long cottony hair which completely hides the stem and almost hides the leaves; leaves very numerous, linear, about 2 mm. long, closely appressed to the stem and very densely imbricate, glabrous, blunt at apex; no venation obvious on either surface; peduncles solitary, terminating the stem, very slender or subfiliform, 5–6 mm. long, very sparsely white-pilosulous or glabrous and shiny; heads solitary, hemispheric, about 2 mm. in diameter, few-flowered; involucral bractlets 2 or 3, ovate, about 2 mm. long and wide, acute at apex, brunneous, glabrous, shiny; staminate florets: sepals 3, firm and rigid, dark-brown or blackish, elliptic, about 2 mm. long and 0.7 mm. wide, acute or short-acuminate at apex and bearing a dense tuft of villous erect hairs on the back at the apex; petals united into a membranous 3-lobed tube about 1.5 mm. long, the lobes sharply acuminate or apiculate, glabrous; stamens 3, exserted; pistillate florets: sepals 3, practically separate to the base, elliptic, dark-brown or blackish, firm and rigid, navicular, about 2.2 mm. long and 1 mm. wide, sharply acute at apex, very densely villous with an erect tuft of whitish hairs at the apex on the back; petals 3, separate, elliptic, navicular, about 2.2 mm. long and 0.8 mm. wide, firm, somewhat stramineous, subtranslucent, subacute, eglandular, densely white-villous with erect white hairs from the middle to the apex; ovary conspicuously 3-lobed, about 1 mm. long and wide, glabrous, plainly 3-celled; style-branches 3, linear, about 1.2 mm. long, white, papillose at apex; stigmas 3, linear, about 1.4 mm. long, simple, unbranched.

COLOMBIA—BOYACÁ: Cordillera oriental, Nevadodel Cocuy, high valley of Las Lagunillas, alt. 4000–4300 m., *José Cuatrecasas 1537*, September 12, 1938, TYPE; in the United States National Herbarium at Washington.

Paepalanthus paramensis Moldenke, sp. nov. Herba acaulis; foliis caespitosis graminoideis valde villoso-pilosis; vaginis late cylindricis subglabris vel sparsissime pilosis, ad apicem subtruncatis undulatis; pedunculis mediocriter tenuibus, versus apicem dense villoso-pubescentibus, versus basim glabrescentibus; capitulis compositis griseis.

Stemless herb; leaves tufted, olivaceous, grass-like, 2.5–6 cm. long, 2–6 mm. wide, broadest at the base, sharply subulate-tipped at apex, entire, abundantly villous-pilose with long, whitish, shaggy, spreading hair on both surfaces, many-nerved, not fenestrate; sheaths rather broadly cylindric, about 2.5 cm. long, subglabrous or very sparsely pilose with widely scattered hairs, especially at the apex; mouth subtruncate, almost regular, the margins slightly flaring and undulate-lobed; peduncles medium-slender, 4–8 per plant, 5–7 cm. long, densely villous-pubescent with incanous spreading hairs toward the apex, much more sparsely so or glabrescent at base; heads hemispheric or almost spherical, 1–1.4 cm. in diameter, ashy-gray, compound, composed of about 6 smaller sessile heads; involucral bractlets brunneous, broadly oblong or ovate, about 3.5 mm. long and 3.4 mm. wide, usually 2-lobed at the broadly rounded apex, truncate at base, lightly villosulous-pilose toward the apex outside; receptacular bractlets oblong, about 2.9 mm. long and 1.4 mm. wide, subacute at apex, densely villous on the back toward the apex, with a dense tuft of erect hair at the very apex; staminate florets: short-pedicellate; sepals 3, brown, connate at the very base, obovate, about 2.4 mm. long and 0.9 mm. wide, rounded or subacute at apex, cuneate at base, densely white-villous at the apex on the back with an erect conspicuous tuft of hair; free portion of petals narrow-elliptic, hyaline, about 1.2 mm. long and 0.5 mm. wide, acute at both ends, eglandular, connate at base only, glabrous; stamens 3, about 1.4 mm. long, the filaments white, anthers yellowish; pistillate florets: short-pedicellate; sepals 3, brown, obovate, about 1.9 mm. long and 0.9 mm. wide, subacute at apex, densely villous on the back with a conspicuous tuft of white erect hair at the apex; petals 3, hyaline, free, elliptic, about 0.9 mm. long and 0.4 mm. wide, very densely tufted-villous on the back; pistil about 1.2 mm. long; styles, stigmas, and style-appendages 3 each; ovary minutely puberulent.

COLOMBIA—NORTE DE SANTANDER: Páramo del Hatico, en route from Toledo to Pamplona, alt. about 2900 m., *E. P. Killip & A. C. Smith 20,622*, March 12 or 13, 1927, TYPE; in the United States National Herbarium at Washington.

Paepalanthus viscosus Moldenke, sp. nov. Herba perennis; caule tenui dense folioso bifurcato; foliis linearibus viscidis villosis glabrescentibus; vaginis adpressis albido-villosis glabrescentibus, ad apicem oblique lobatis; pedunculis filiformibus stramineis 2-costatis densiuscule piloso-pubescentibus; capitulis griseis.

Perennial herb; stems slender, 1–3 cm. long, apparently creeping, rooting at the nodes, very leafy, bifurcate; leaves olivaceous, linear, viscid, 5–10 mm. long, 0.5 mm. wide or less, blunt at apex, shaggy-villous when young and toward the base, glabrescent in age, closely imbricate and appressed to the stems when young, more divaricate in age, 1-nerved, often canaliculate, not fenestrate; sheaths narrow, closely appressed to the peduncles, 6–12 mm. long, white-villous with long divergent hair, glabrescent in age, its mouth very obliquely lobed, the lobe narrow-lanceolate, about 2 mm. long, slightly divergent, acuminate; peduncles very slender or filiform, stramineous during anthesis, later brunnescent, 2-costate, hardly twisted, 4–7 cm. long, rather densely pilose-pubescent; heads gray, hemispheric, 2–4 mm. wide; involucral bractlets stramineous, ovate, about 0.7 mm. long and 0.4 mm. wide, acute at apex, glabrous; receptacle densely long-villous; receptacular bractlets oblong, about 1.4 mm. long and 0.5 mm. wide, obtuse at apex, stramineous in the center, hyaline at the margins, tufted-villous at the apex on the back; staminate florets: short-pedicellate; sepals 3, connate at the very base only, obovate, about 1 mm. long and 0.5 mm. wide, rounded at apex, cuneate at base, tufted-villous at the apex on the back; petals 3, connate into a hyaline, hollow, eglandular, glabrous, minutely 3-lobed tube; stamens 3, about 1 mm. long, white; pistillate florets: short-pedicellate; sepals 3, connate at the base only, stramineous, obovate, about 0.9 mm. long and 0.4 mm. wide, glabrous except for 2 or 3 erect villous hairs at the apex (or densely tufted) on the back; petals 3, free, hyaline, narrow-elliptic, about 1.2 mm. long and 0.3 mm. wide, acute at apex, tufted-villous on the back at the apex; pistil about 1.2 mm. long; styles, stigmas, and style-appendages 3 each; ovary glabrous.

SURINAM: Sandrij I, *William Andrew Archer 2836* between November 14 and 25, 1934, TYPE; in the United States National Herbarium at Washington. The collector describes the leaves as sticky.

SYNGONANTHUS CAULESCENS (Poir.) Ruhl. var. **angustifolius** Moldenke, var. nov. Haec varietas a forma typica speciei recedit foliis longioris angustioris 2–3.5 cm. longis, 0.5–2 mm. latis, ad apicem attenuatis argute acutis.

This variety differs from the typical form of the species in its uniformly longer and narrower leaves, which are 2–3.5 cm. long and 0.5–2 mm. wide, gradually attenuate to the sharply acute apex.

COLOMBIA: Los Llanos, Méta, in a bog about 20 km. south and 30° west of Orocué, alt. about 150 m., *Oscar Haught 2747*, April 9, 1939, TYPE; in the Britton Herbarium at the New York Botanical Garden. It is said to be a common herb in bogs of the Llanos region. The typical form of the species is well represented by *Haught 2355* from Magdalena.

SYNGONANTHUS CAULESCENS (Poir.) Ruhl. var. **procerus** (Klotzsch) Moldenke, comb. nov. *Paepalanthus procerus* Klotzsch in Schomb., Reise in Brit. Guian. **3**: 1115. 1848.

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BULLETIN
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STUDIES IN THE WORONINACEAE—II. THE CYTOLOGY OF OLPIDIOPSIS ACHLYAE SP. NOV. (AD INT.)

D. A. McLARTY

(WITH EIGHTY-ONE FIGURES)

INTRODUCTION

Sexuality in the Chytridiales was first demonstrated by Cornu (1872) in the formation of *Olpidiopsis* resting spores. This fusion of thalli of unequal size has stimulated the interest of many mycologists and has led to the view that members of this genus may be ancestral to the Saprolegniales. Few critical observations, however, have been made on resting spore formation in any of these species. Life cycle studies and observations on plasmogamy in the formation of resting spores have been made by Reinsch (1878), Fischer (1880, 1882), Dangeard (1890), Maurizio (1895), Butler (1907), and others for various species of *Olpidiopsis*. The most complete cytological study which has been made on this genus, however, was published by Barrett in 1912. His studies include observations on the penetration of the host and the developmental stages of the zoosporangia and resting spores in three species of *Olpidiopsis*. He has demonstrated that the male and female thalli are multinucleate when plasmogamy occurs and states that the resting spore, at maturity, contains many small nuclei. His illustrations of these stages, however, leave much to be desired. Moreover, he has not demonstrated the fate of the supernumerary male nuclei which may enter the female thallus from several smaller thalli nor has he shown conclusively that karyogamy occurs in the formation of the so-called sexual resting spores. At that time sexuality was looked upon as a well developed, constant feature in *Olpidiopsis* species and this may have influenced somewhat Barrett's interpretation of certain paired nuclei which he observed and illustrated.

Inasmuch as karyogamy in the incipient resting spores of *Olpidiopsis* has not been proven, the true significance of plasmogamy, which has been so often observed and discussed, and the importance of *Olpidiopsis* species in taxonomic considerations remain unknown. Consequently, a general cytological study of *O. Achlyae* has been made with particular reference to the formation of its sexual and asexual resting spores.

[THE BULLETIN FOR JANUARY (68: 1–74) WAS ISSUED DECEMBER 31, 1940]

As reported in a previous paper (McLarty 1941), cultures of *Achyla flagellata*, parasitized by *O. Achlyae*, were maintained on boiled hemp seeds in sterile charcoal water. Consecutive stages in the penetration of the host and the subsequent development of zoosporangia and resting spores were studied from the living material in hanging-drop cultures.

For the study of the highly refractive material which is commonly present in the thalli of *O. Achlyae* at all stages of development, osmic acid, Sudan III, xylene, and acetone were used, while the cell walls were tested for cellulose with zinc chloroiodide and Gram's solution accompanied by sulphuric acid.

For cytological study of fixed and stained material entire hemp-seed cultures were killed in a variety of standard fixatives at full strength and in various dilutions. Dilute fixatives used for 48 hours gave the best results. Flemming's strong and medium solutions diluted to one quarter and Flemming's weak diluted to one half were most widely used. Nawaschin's fixative gave the best fixation of the host protoplasm. The material was embedded in paraffin, and sections were cut 2–4 μ thick and usually stained with Heidenhain's haematoxylin and Flemming's triple stain. Although the former was useful in the study of the zoosporangium, it was necessary to rely entirely upon the triple stain to differentiate the structures and inclusions of the resting spores.

OBSERVATIONS

The Structure and Germination of the Zoospore. When in motion the zoospore is oval, sometimes reniform in shape, and possesses two equal flagella which are laterally attached near the anterior end (fig. 1*a*, *b*, *c*). In swimming the spore travels with a slight swaying motion as it turns over on its axis in a fashion similar to that described for zoospores of *Thraustotheca clavata* and *Pythiella vernalis* by Weston (1918) and Couch (1935), respec-

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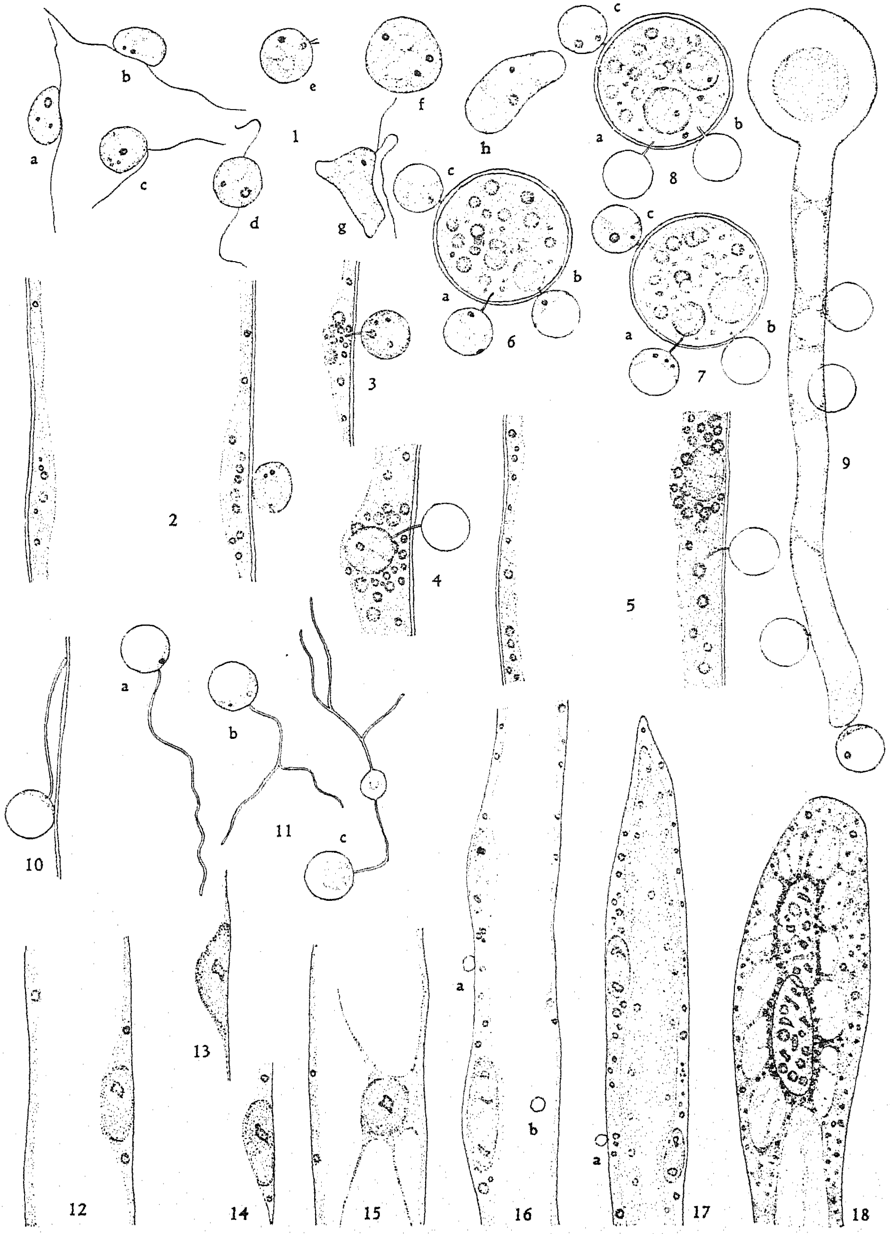
Explanation of figures 1–18.

FIG. 1. Zoospores drawn from living material showing refringent globules and vacuoles in finely granular protoplasm; *a–c*, zoospores in motion; *d–g*, zoospores at rest showing the changes in shape, retraction of flagella, and amoeboid movements which may occur. × 1730. FIGS. 2–5. Progressive stages in the penetration of the host by the zoospore and the entrance of the parasite thallus into the host protoplasm. × 1730. FIGS. 6–8. Progressive stages in the penetration of an encysted *Achlya* zoospore by three *O. Achlyae* zoospores. Spore *c* failed to liberate its contents. FIG. 9. A degenerated *Achlya* zoospore which had begun to germinate in water and into which four *O. Achlyae* zoospores had penetrated. FIG. 10. A germinating *O. Achlyae* zoospore whose penetration tube failed to enter the host cell. FIG. 11. *O. Achlyae* zoospores germinating in water in the vicinity of *Achlya* filaments. × 1730. FIGS. 12–15. Progressive amoeboid-like changes in shape brought about in a very young thallus by the streaming of the host protoplasm. × 1270. FIGS. 16–17. Young thalli suspended in the peripheral layer of host protoplasm. × 540. FIG. 18. Two slightly older thalli which have taken up a more or less fixed position in the tip of an *Achlya* filament and have begun drawing the host protoplasm about them. Some localized swelling of the *Achlya* filament is evident. × 540.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tively. Upon coming to rest, even momentarily, the zoospore tends to assume a spherical shape (fig. 1*c*, *e*) and at such time the attachment of the flagella at one point can often be observed in living material, although treatment with Gram's solution or osmic acid is often needed to bring out these details sharply. The protoplasm of living zoospores appears faintly brown and slightly granular, with one or several highly refractive, small bodies which give a brilliant fat reaction with Sudan III. In some cases a refringent body is visible at the base of the flagella, as Barrett (1912) has reported.

Zoospores which have been fixed and stained (figs. 44, 45) contain somewhat vacuolate, slightly granular cytoplasm. The most prominent structure in the spore is the large resting nucleus with a prominent central nucleolus. Fairly dense regions in the cytoplasm probably represent remnants of oil bodies.

As the zoospores escape from the mouth of the exit tube they swim directly away without showing any tendency to encyst as do the spores of *Ectrogella*, *Aphanomycopsis*, *Pythiella*, *Achlya*, etc. After an active period varying from a few minutes to one-half hour the spores may come to rest, round up, and in many cases retract their flagella (fig. 1*e*, *f*, *g*). After a period of a few or several minutes, during which the zoospore may assume various shapes (fig. 1*f*, *g*, *h*), it regains its spherical shape, the flagella reappear without change in position, and the spore swims away. Although one or more rest periods may occur during the motile existence of the spore, diplanetism does not seem to be as well defined in *O. Achlyae* as in other members of *Olpidiopsis* (Butler 1907; Barrett 1912). So far encystment of the type found in diplanetic Oomycetes has not been observed in this species. It was originally suggested by Butler (1907) that this occurrence of a period of rest during the swimming period of the zoospores of Chytrideaceous species may represent primitive diplanetism. Supporting this viewpoint, Atkinson (1909) considers diplanetism in certain species of the Chytridiales and Lagenidiales (Karling 1939) to be strong evidence of phylogenetic relationships between the higher Oomycetes and these simpler fungi. The recent discovery of diplanetism in *Ectrogella*, *Aphanomycopsis*, and *Pythiella* by Scherffel (1925) and Couch (1935) helps to complete the diplanetic series through *Lagenidium* and *Myzocytium* (Zopf 1884) to species of *Pythium* (de Bary 1860) and the higher Oomycetes. At any rate these periodic pauses probably allow the spore to remain viable over greater periods than would otherwise be possible. Zoospores of *O. Achlyae* have been known to remain viable in sterile charcoal for 48 hours.

After swimming for an hour or occasionally for a much longer period, the zoospore settles down on the surface of the host, retracts its flagella (fig. 2), and after exhibiting amoeboid motion for several minutes, rounds up and becomes invested by a definite wall. The protoplasm becomes greyish and somewhat more granular, and within an hour or less the spore will infect the host or die. A very fine penetration tube is formed at the point of contact with the host (fig. 3), elongates, and usually raises the zoospore slightly from the surface of the host. Penetration appears to take place by local dissolution of the host wall rather than by mechanical action. It is not possible to view the passage of the spore protoplasm through the penetration tube but, under favorable conditions, the movement of the protoplasm out of the spore case and its emergence from the broken end of the exit tube may be observed (figs. 3, 4). After remaining attached for a few minutes, the tiny, slightly vacuolate thallus is carried away in the streaming host protoplasm, where it may be visible for a time before the refringent bodies of the host surround and obscure it from view (fig. 5).

Fischer (1882) suggested that the host may secrete some substance by which the zoospores of the parasite are either repelled or attracted. Zoospores of *O. Achlyae*, germinating in water near *Achlya* filaments, show no tendency to orientate their penetration tubes in the direction of the host. Moreover, abortive penetration tubes have frequently been found growing into empty zoosporangia of the host, while zoospores in contact with the host may produce long penetration tubes which fail to penetrate (fig. 10). This does not appear to be due to rigidity of the wall of the filament, for penetration of encysted zoospores of the host by *O. Achlyae* spores has often been observed (figs. 6–8).

So far it has been impossible to germinate the zoospores on any artificial medium. Spores were often observed, however, germinating in water in the vicinity of *Achlya* filaments (fig. 11), producing long, slender, simple or branched penetration tubes which failed to open. Some such spores (fig. 11c) appear similar to germinating spores of *Diplophlyctis*, *Entophlyctis*, *Nephrochytrium*, and *Endochytrium* (Karling 1930, 1931, 1938; Hillegas 1940). In the limited number of individuals observed in *O. Achlyae* it was impossible, however, to determine whether or not the nucleus migrated into this swelling on the germ tube as it does in the species referred to above.

Development of the Zoosporangium. About ten hours after penetration, the young thalli become readily visible as rather hyaline bodies of the definite shape, in the peripheral protoplasm of the host. Their protoplasm is very faintly granular and a few highly refractive bodies, which stain brilliant red with Sudan III and blacken with osmic acid, are usually visible (figs. 16, 17). At this early developmental stage no structural, cellulose wall could be demonstrated by plasmolytic methods or by treatment with zinc chloroiodide. The thalli, however, are surrounded by a definite membrane which sharply outlines the parasite and makes it clearly distinguishable from the host protoplasm. The shape which these young thalli assume foreshadows that of the mature sporangium. In this regard the thallus differs markedly from that of

Woronina species (Cornu 1872; Fischer 1882; Cook and Nicholson 1933; and others) in which the plasmodium has been described as being naked and quite indistinguishable from the host protoplasm. The formation of zoosporangia from monospore infections, moreover, shows conclusively that plasmodia are not formed in *O. Achlyae* by the fusion of several thalli within the host cell. This confirms the belief of Fischer (1882) and Barrett (1912).

During these early stages of development the thalli behave as passive inclusions in the host and may be carried back and forth in the streaming protoplasm. Depending apparently upon the activity of the host protoplasm, the thalli may develop near the point of infection or they may be carried along and accumulated in localized terminal or intercalary swellings (figs. 18, 19). Fischer (1880), Diehl (1935), and others have maintained that very young thalli of *Olpidiopsis* species may exhibit amoeboid motion. No indication of such activity on the part of young thalli of *O. Achlyae* has been found. Some which remained stationary against the wall of the filament while the host protoplasm streamed rapidly by, exhibited rapid changes in shape and became momentarily elongated in the direction of the flow (figs. 12–15).

When the thalli could be seen clearly, it was obvious that these movements were entirely passive and due to tensions set up by the streaming host protoplasm.

As the thalli increase in size the fatty bodies increase in number and in size and impart a granular, yellowish appearance to the protoplasts which,

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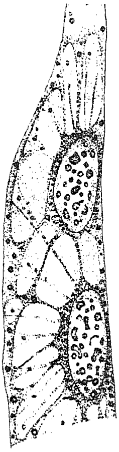
Explanation of figures 19–35.

FIGS. 19–29. Progressive stages in the development and maturation of two *O. Achlyae* zoosporangia. × 630. FIG. 19. Two incipient zoosporangia of *O. Achlyae* containing numerous, irregular fatty masses. FIGS. 20–21. Progressive stages in the dispersal of the fatty masses and the concomitant formation of vacuoles in the thalli. FIG. 22. Coalescence of smaller vacuoles to form larger central vacuoles; exit tube of sporangium A is indicated by a slight protuberance. FIG. 23. Sporangia with homogeneously granular protoplasm showing the vacuolar transformations which occur. FIG. 24. Formation of centrifugal cleavage furrows at *x* and *y*. FIG. 25. Sporangium A containing zoospore initials surrounding irregular vacuolar areas. FIG. 26. Sporangia in the homogeneous stage following cleavage during which the lines of demarkation between zoospore segments are invisible; the vacuole-like spaces have regained their even margins. FIG. 27. The reappearance of the zoospore segments by a rounding up of the individual initials. FIG. 28. Zoospores preparing to swarm within the sporangium following the disappearance of the vacuole-like spaces. FIG. 29. Mature zoospores swimming out through the ruptured exit tube of sporangium *A*; sporangium *B*, in the homogeneous stage, is undergoing a period of rest. FIG. 30. Incipient zoosporangia, in the early vacuolate stage, developing fine bristles on their surfaces. × 540. FIGS. 31–32. Very young uninucleate thalli of *O. Achlyae* stained with haematoxylin. × 1660. FIG. 33. Three young thalli of the parasite floating freely in the host protoplasm; lines of flow indicate that the latter was actively streaming when fixation took place. × 1660. FIG. 34. A slightly older sporangium stained with haematoxylin showing resting nuclei suspended in finely granular protoplasm which exhibits irregular spaces which were occupied by fatty masses in the living condition. × 1660. FIG. 35. A portion of a sporangium which was fixed in an early stage of vacuole formation. × 1660.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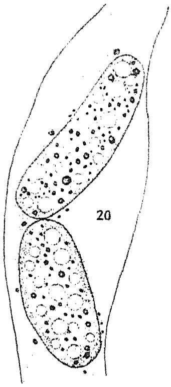
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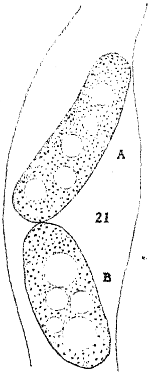
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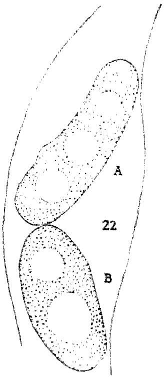
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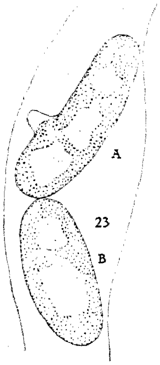
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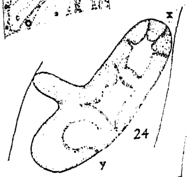
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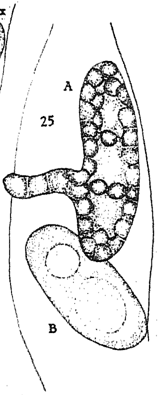
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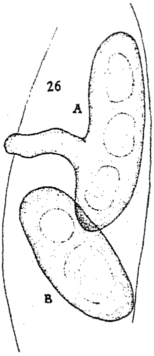
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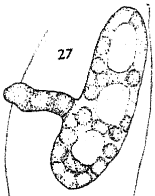
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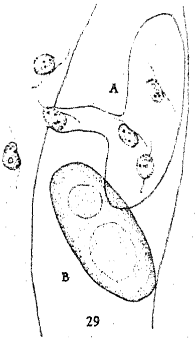
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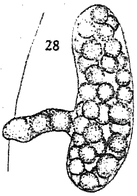
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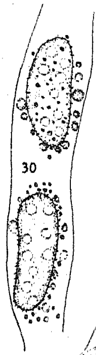
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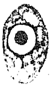
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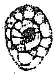
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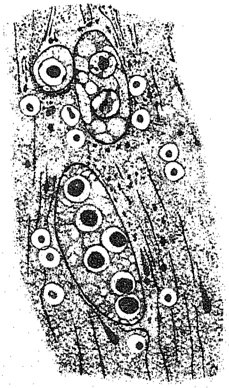
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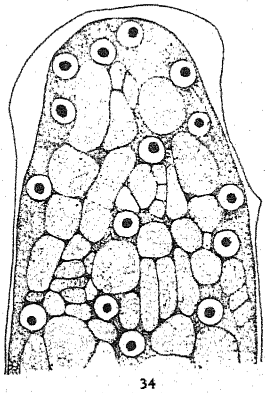
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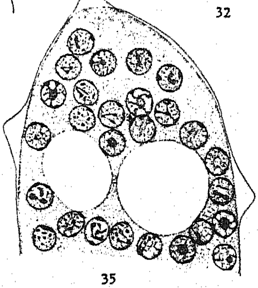
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at the same time, become surrounded by a membrane which gives a positive cellulose reaction with zinc chloroiodide. In the meantime the host filament usually becomes enlarged around the thalli, and the host protoplasm becomes highly vacuolate with radially arranged cytoplasmic strands (figs. 18, 19) connecting the peripheral host protoplasm with the dense layer of degenerating protoplasm immediately surrounding the parasite. As the thallus continues to grow streaming of the host protoplasm may be observed and granules may be seen flowing in toward it from all sides. Finally all the visible host protoplasm is absorbed by the thallus. Within the parasite the refringent bodies gradually become broken up and appear as oily droplets suspended in a more homogeneous protoplasm. At this stage of development, small vacuoles make their appearance in the thallus (fig. 20). As these vacuoles become more distinct they begin to coalesce, while the dispersion of the fatty material becomes more complete. At this stage the protoplasm of the parasite appears granular and light brown in color, owing to the small, fatty bodies dispersed throughout it. Sudan III when applied to such thalli stains the protoplasm brick-brown. Cook and Nicholson (1933) demonstrated that fatty material in *Woronina polycystis* became converted into proteins at this stage. Millon's reagent, however, failed to indicate a similar condition in *O. Achlyae.*

Up to this point the elaboration and dispersion of fatty material in the sporangia of *O. Achlyae* is essentially similar to what has been described in most chytrid species. In the latter, however, coalescence of the droplets occurs before cleavage takes place. Consequently the protoplasm becomes hyaline and each zoospore receives one large refringent globule. In *O. Achlya*, as well as in other members of the genus and in Saprolegniaceous species, the refringent bodies do not coalesce and, as a result, when zoospore initials are delimited, each one includes several tiny droplets which impart a granular appearance to the protoplasm.

Further developmental stages of these two thalli were observed and illustrated at various time intervals (figs. 21–29). At 10:00 p.m. vacuoles were clearly visible in the thalli (fig. 21). Fusions between vacuoles occurred until, at 10:16 p.m., the thalli appeared as illustrated in figure 22. At the same time the rudimentary exit tube made its first appearance on sporangium *A* as a small, hyaline protuberance and began to grow toward the host wall. Fifty minutes later the vacuoles began to undergo changes in shape (fig. 23) which continued for fourteen minutes before the cleavage furrows began to run out from the vacuoles to the plasma membrane (fig. 24*x, y*).

At this point our observations differ from those of Schwarze (1922) for *O. Saprolegniae* in that the spaces previously occupied by the vacuoles did not disappear when the cleavage furrows cut through the plasma membrane. Consequently, for about one minute following the completion of cleavage, the zoospore initials remained faintly visible flanking the irregular vacuolar spaces (fig. 25*A*). Then, as the protoplasm became homogeneously granular and somewhat oleaginous, the outlines of the zoospore initials disappeared and the vacuole-like spaces regained their even contours (fig. 26*A*, *B*). During the process of cleavage there was no indication of loss of water or fatty material from the spore segments comparable to what Harper, Bold, and others describe. The disappearance of the lines of demarkation, however, is probably due to increase in size through rehydration as Harper (1899, 1914), Schwarze (1922), and Karling (1937b) have described.

While these developments were taking place within the sporangium, the exit tube continued to grow until it came in contact with the host wall (fig. 24). Subsequent growth of the tube caused the sporangium to shift its position in the filament although the latter remained free in the hypha and did not become lodged against the opposite wall. Consequently, the tip of the exit tube could not exert pressure on the host wall. Furthermore, no appressorium-like attachment organ, which might have allowed the tube to pierce the filament mechanically, was observed. The host wall appeared to dissolve at the point of contact with the exit tube and the latter moved through to assume the position shown in figure 25*A*.

Sporangia in the condition illustrated in figure 26*A*, *B* may undergo a prolonged rest period before liberating their zoospores. That the segments do not become confluent during this rest period, as Büsgen (1882) and Butler (1907) believed, may easily be demonstrated by slightly plasmolyzing sporangia in this condition.

After a rest period of 43 minutes the spore segments became visible again (fig. 27). Twenty minutes later the vacuole-like spaces suddenly disappeared and the spores, becoming somewhat larger and assuming their mature shape, began to swarm in the sporangium (fig. 28). After a swarming period which lasted only for three minutes the tip of the exit tube burst and the zoospores emerged fully formed and swam away (fig. 29*A*). The spores may swarm in the sporangium for thirty minutes or more.

The first spores to leave the sporangium seem to be forcefully ejected by pressure within it sufficient to burst the exit tube and to expel an initial mass of spores a considerable distance from the end of the exit tube. It has been noticed that bacteria tend to accumulate around the tips of newly opened exit tubes and subsequently to infest the empty sporangia. This suggests the presence of some attractive, hyaline osmotic fluid in which the spores have been bathed. Karling (1937a) observed similar hyaline material accompanying the zoospores of *Endochytrium operculatum* as they emerged from the sporangium.

As has been pointed out above, the piercing of the plasma membrane by the cleavage furrows in sporangia of *O. Achlyae* does not lead immediately to the loss of the vacuolar sap and the consequent disappearance of the vacuolar spaces. Bold (1933) likewise illustrates a vacuole-like space surrounded by multinucleate segments of protoplasm which have been cut out by the primary cleavage furrows in *Protosiphon botryoides*. As is shown in figures 41 and 42 from stained material, neither a continuous plasma membrane nor a tonoplast bounding the vacuole-like spaces is demonstrable after cleavage has been completed. In spite of this, the sporangia of *O. Achlyae* have been found to maintain their size and, when the zoospores are liberated, have shown evidence of osmotic pressure within the sporangium.

When fixed and stained, the protoplasm of young, uninucleate thalli appears finely granular and rather vacuolate (figs. 31, 32). In figure 33 a uninucleate and a binucleate thallus are shown, with a larger thallus with six nuclei which is presumably an eight-nucleate stage two of whose nuclei lie in another section. This appears comparable to the thalli shown in figures 16 and 17. Although the margin of the thallus is well defined no structural wall is present at this stage of development. The protoplasm of the parasite appears to be fairly vacuolate even though no vacuoles are discernible in the living thalli at this stage. The irregular shape of these vacuole-like spaces, in conjunction with observations on living material, suggests that they merely represent the spaces left in the protoplasm as a result of the dissolution of the fatty material by the fixing agents. A slightly older thallus, probably comparable to those shown in figure 19, is illustrated in figure 34. The thallus now has a definite cellulose wall and the finely reticulate protoplasm contains many irregular vacuole-like spaces which are presumably caused by the distortion and dissolution of the fatty masses during the process of fixation. This is probably the highly vacuolate stage which Dangeard (1890) describes for *O. Saprolegniae*. A stage which is probably comparable to that shown in figure 21 is illustrated in figure 35. The high degree of dispersion of the fatty bodies at this stage of development undoubtedly prevents the distortion of the protoplasm in the course of fixation. Numerous nuclei and clearly defined vacuoles are present in the finely reticulated protoplasm. A later stage, in which all the vacuoles have fused to form a single, large, central vacuole, is shown in figure 37. Judging by the rather uniform distribution of the nuclei throughout the reticulate protoplasm, sporangia in this condition are ready to undergo cleavage. In large sporangia with relatively small central vacuoles, primary cleavage furrows may first cut out large multinucleate masses (fig. 38) as in *Synchytrium decipiens, Pilobolus Crystallinis, Didymium melanospermum* (Harper 1899, 1914) and *Protosiphon botryoides* (Bold 1933). Later uninucleate protoplasts are delimited by secondary furrows. The failure of Schwarze (1922) to believe that such multinucleate masses may be delimited may be due to the fact that he observed cleavage in small thalli similar to those shown in figures 39 and 40. It is to be noted in figure 38 that the nuclei are in the process of division.

A smaller sporangium with a single large central vacuole is shown in figure 39, in which cleavage furrows are evident, arising at the tonoplast as broad V-shaped clefts between pairs of nuclei. At a slightly later stage (fig. 40), the centrifugal furrows have reached the plasma membrane. The uninucleate segments, bordering the vacuolar space, give the latter a scalloped margin similar to that in figure 25*A*. Sporangia fixed during the rest period which follows cleavage are illustrated in figures 41 and 42. Angular, uninucleate segments surrounding clear areas, which are comparable in position to the vacuoles of younger thalli, are clearly evident although no tonoplasts or plasma membranes are discernible. It is to be noted that in his Figure 39, Plate 24, Barrett (1912) has illustrated a similar condition although he does not mention the absence of the tonoplast and describes it simply as a "vacuolate resting condition."

After this period of rest, the segments shrink and suddenly reappear as dense masses of protoplasm. If the earlier stages had not been observed, this phenomenon might give the impression of simultaneous cleavage. The erroneous reports by Barrett (1912) and others of cleavage of this type may be due to a misunderstanding of this stage. When the vacuole-like spaces disappear, the initials enlarge, become somewhat vacuolate (fig. 43), develop flagella, and begin swarming in the sporangium.

Nuclear Division. Nuclear division in *O. Achlyae* is mitotic and, as in the sporangia of most of the lower fungi which have been cytologically investigated, is simultaneous (figs. 37, 75). In the resting condition the nuclei are spherical or slightly oval and contain a centrally placed, deeply-staining nucleolus (fig. 46). Nuclei containing definite nucleoli do not usually exhibit chromatin reticula similar to those described by Karling (1937b) in *Cladochytrium replicatum*. Delicate strands, which with Flemming's triple stain appear blue in contrast to the brilliant red of the nucleolus, have often been observed radiating out from irregular shaped or vacuolate nucleoli (figs. 47–49). In some nuclei with definite, radiating reticula, dense, blue-staining segments have been observed in the periphery of the nucleoli (fig. 49).

These observations suggest that the nucleolus in this species functions as a storehouse of chromatin like that which has been described by Wager (1913), Curtis (1921), Kusano (1907a, 1907b, 1930) in *Polyphagus Euglenae*, *Synchytrium endobioticum*, *S. Pueriae*, and *S. fulgens*. Although definite extrusions, similar to those described by Miss Curtis, have not been seen, the orientation of the chromatin net work upon the nucleolus, the vacuolation and differential staining properties of the latter, together with the early disappearance of the nucleolus during mitosis suggest, at least, a close association of the latter with the formation of the chromosomes. In *Cladochytrium replicatum* (Karling 1937b) and *Endochytrium operculatum* (Hillegas 1940) the nucleolus has been found to persist well through the metaphases, apparently taking little or no part in the elaboration of the chromosomes.

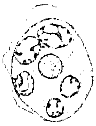
The appearance of radiating chromatin threads has been taken to indicate the beginning of the prophases. In later stages the chromatin is evident as globular (figs. 50, 52) or rod-like masses (fig. 51) distributed throughout the karyoplasm. In late prophase the nucleolar material is usually absent.

Concomitant with the formation of the chromosomes is the production and division of a centrosome-like body similar to that described by Harper (1895, 1905) for *Erysiphe* and *Phyllactinia* (fig. 50, 53–57). The chromatin material, however, has shown no tendency to be orientated upon these bodies nor has any marked development of astral radiations been observed (fig. 56).

The chromosomes, at the close of the prophases, become arranged in a ring about the margin of the equator of the spindle. In some nuclei this arrangement is evident in profile views of the metaphases (fig. 62), but most commonly the chromosomes are crowded together and appear as a dark line (fig. 61). At this stage the nucleus becomes somewhat elongate and the centrosomes at the poles of the spindle are clearly evident.

Explanation of figures 36–67.

FIG. 36. A small sporangium containing five nuclei, two of which are unusually large. × 1655. FIG. 37. A sporangium nearing maturity with a single large vacuole and reticulate protoplasm with numerous, rather evenly spaced nuclei. × 1655. FIG. 38. Primary cleavage furrows delimiting multinucleate protoplasmic masses. × 1170. FIGS. 39–40. Small sporangia stained with Flemming's triple stain showing the origin of the cleavage furrows at the tonoplast and their progressive centrifugal development out to the plasma membrane. × 1655. FIGS. 41–42. Zoosporangia which were fixed during the homogeneous stage and stained with haematoxylin. × 1170. FIG. 43. Incipient zoospores of *O. Achlyae* fixed within the sporangium and stained with Flemming's triple stain to show distinct chromatin masses scattered throughout the nuclei; nucleolar material is present only in zoospore *A*. × 2150. FIGS. 44–45. Mature zoospores of *O. Achlyae* with conspicuous nucleoli within the nuclei and very little chromatic material. × 2150. FIG. 46. Resting nucleus of *O. Achlyae* with a prominent central nucleolus surrounded by hyaline karyoplasm. × 3100. FIG. 47. An early prophase stage with an irregular nucleole from which faint chromatin strands radiate. × 3100. FIG. 48. A prophase stage showing a chromatin network surrounding a vacuolate nucleole. × 3100. FIG. 49. A prophase stage stained with Flemming's triple stain showing chromatin material surrounding a ruby red nucleolus in which blue crescentic chromatin masses are evident. × 3100. FIGS. 50–51. Prophases with spherical and rod-like chromatin masses, respectively, without nucleolar material; a single central body is present on each nuclear membrane. × 3100. FIG. 52. A prophase stage showing six chromatin masses and two polar bodies on the nuclear membrane. × 3100. FIGS. 53–55. Stages in the division of the central body and the migration of the daughter bodies to the poles of the nucleus. × 3100. FIG. 56. A prophase stage showing polar bodies with a few astral rays. × 3100. FIG. 57. A nucleus with central bodies arriving at the poles and with scattered chromatin masses. × 3100. FIGS. 58–59. Polar views of equatorial plate stages with six chromosomes arranged in a ring. × 3100. FIG. 60. Polar view of an equatorial plate stage showing six elongate chromosomes. × 3100. FIGS. 61–62. Profile views of equatorial plate stages showing central bodies at the poles of the spindle. × 3100. FIG. 63. An early anaphase stage; a central body is shown at one pole of the spindle. × 3100. FIGS. 64–66. Progressively later anaphase stages. × 3100. FIG. 67. Late anaphase showing the elongate spindle with what appears to be a remnant of the nuclear membrane to one side. × 3100.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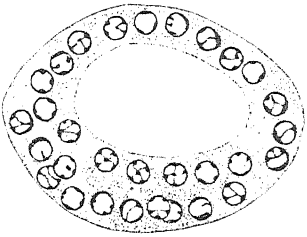
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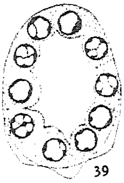
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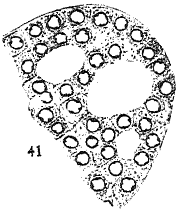
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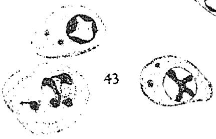
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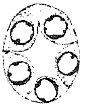
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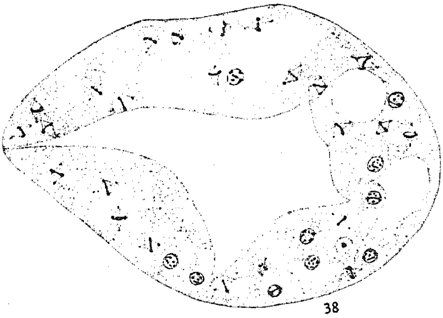

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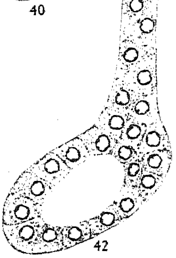
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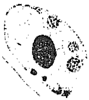
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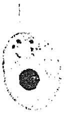
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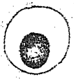
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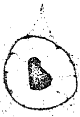
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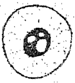
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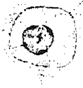
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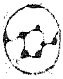
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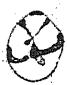
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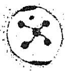
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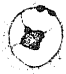
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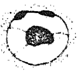
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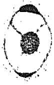
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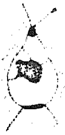
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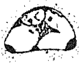
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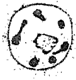
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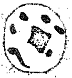
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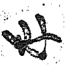
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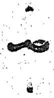
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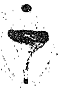
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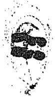
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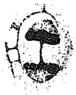
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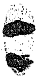
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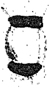
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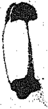
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In polar views of the metaphases (figs. 58–60) six chromosomes in a ring have often been observed. In all favorable preparations studied so far the chromosome number has been constant and the same as the count which Barrett (1912) made for the chromosomes of *O. vexans*. No indication of reduction division has ever been encountered throughout this investigation. It is probable that reduction division in *Olpidiopsis* species takes place at the time of germination of sexual resting spores.

The earliest anaphase which has so far been observed, is illustrated in figure 63 and the chromosomes, which have separated slightly, form two parallel lines near the equator. Later anaphase stages are shown in figures 64–67. Barrett (1912) found that the nuclear membrane in *O. vexans* disappeared during the late anaphase stages. The achromatic spindle in such case would be intranuclear in origin as in most chytrid species which have been examined. In *O. Achlyae* the nuclear membrane may be rather indistinct in the metaphases but the nuclear area is sharply set apart from the surrounding cytoplasm. Although fragments of the membrane may be present during the anaphase stages (fig. 67) the breakdown of the nuclear membrane in *O. Achlyae* apparently takes place during the late metaphase stages. In the late anaphases the spindle becomes much more elongate (fig. 67), forcing the masses of chromatin farther apart. This elongate spindle seems to be typical of the lower fungi and has been described by Blackman (1904), Barrett (1912), Wager (1913), Dodge and Gaiser (1926), Karling (1937*b*) and others for various species of chytrids, smuts, and other fungi.

The formation of the daughter nuclear membranes in the telophases was not observed nor were the stages of interphase reorganization of the nuclei followed. It was found, however, that the nuclei in cleaving sporangia (figs. 39, 40) and in zoospore segments (figs. 41, 42) were uniform in their internal organization and appearance. It was assumed that these are the daughter nuclei of the final nuclear divisions in the sporangia and that they represent telophasic reconstruction stages. In all such preparations studied, the nuclei, when stained with Flemming's triple stain, exhibit chromatin masses about the inner margin of the nuclear membrane with some scattered strands traversing the nuclear cavity (figs. 39–42). No nucleolar material has been observed in any preparations of sporangia in these stages of development. The nuclear organization in immature zoospores (fig. 43) is similar to that just described although (fig. 43*A*) indefinite bodies which take a faint safranin stain have been observed in the nuclei of zoospores which had been fixed while still in the sporangium. Mature zoospores (figs. 44, 45) usually contain nuclei with large, central nucleoli and little, if any recognizable chromatin material. These appearances suggest that the reorganization stages are the reverse of the prophases and that the chromosome substance becomes largely transformed into a nucleolus as Bally (1911), Kusano, and Miss Curtis have described for species of *Synchytrium*.

Development of the Resting Spore. The early developmental stages of the incipient resting-spore thalli appear to be identical with those of the zoosporangia, and it is not until the former have attained considerable size that they are distinguishable. In figure 68 a swollen filament containing two female thalli, one small male cell, and two incipient zoosporangia is illustrated. The female thalli are filled almost completely with conspicuous, highly refractive bodies and are consequently recognizable. The male cell, however, is distinguishable from the zoosporangia only by virtue of its association with the female thallus.

At this stage, previous to the deposition of the exospore, the highly refractive bodies in the female cells stain brilliant red with Sudan III, thus indicating their fatty nature.

In fixed and stained material the female cells are easily recognized by their staining reactions. Varying numbers of spherical bodies, apparently the stroma of fatty masses, are present in thalli fixed at a fairly early stage. These bodies, which usually stain brilliantly with crystal violet, are absent in zoosporangial thalli. With Flemming's triple stain these bodies have a translucency which sets them apart from the remaining contents of the thalli, while with Heidenhain's haematoxylin they show greater affinity for the stain and consequently render the preparation difficult if not impossible to study.

A stained preparation of a young female thallus, somewhat younger than those shown in figure 68, is illustrated in figure 73. Nuclei in the prophases of division are scattered throughout the finely reticulate protoplasm in which a few brightly staining bodies, interpreted as the stroma of fatty masses, are dispersed. A slightly older thallus is shown in figure 74 in which the protoplasm exhibits a mesh-like configuration which seems to be associated with the appearance of fixed protoplasm from which large globules of fat or oil have been dissolved during fixation. The exospore is developing around this thallus, and numerous granules of the host protoplasm are present. Dark-staining lines of deposition may be seen extending centripetally within the exospore.

Successive stages in the development of the thalli shown in figure 68 are shown in figures 69–72. In figure 69 some tendency for the fatty masses to increase in number and decrease in size is noted. Hyaline and slightly amber-colored amorphous layers have appeared around the female thalli, replacing in part the dense layer of host protoplasm.

In figure 70 all the host protoplasm surrounding the female thalli has disappeared and the latter are now enveloped by thick, hyaline layers which constitute the exospores. In sporangium *X* several broad-based spines have been evolved within the area of the amorphous layer and the outer limit of the latter is indicated in part by a faint line joining the apices of three of the spines. In the same figure the first stage in the development of the endospore is visible. This appears to first involve a retraction of the granular contents from the original wall to form a hyaline layer which eventually becomes a definite, double-contoured wall (fig. 71*X*). The contents of the female thalli have become more dense and finely granular by the progressive dispersal of the fatty masses shown in figure 69. The male cell likewise contains numerous small refringent bodies. At this stage the fusion of the thalli is about to occur. The highly vacuolate condition of the male and female thalli described by Barrett (1912) has seldom been observed.

Figure 75 illustrates a haematoxylin-stained preparation of a spore comparable to that shown in figure 70*X*. The nuclei are in the equatorial plate stages of division. Vacuole-like spaces are evident in the protoplasm which doubtless represent the regions previously occupied by fatty material. There is no indication of the exospore in this preparation. Figures 78 and 79 represent incipient sexual resting spores stained with Flemming's triple stain which are comparable to figure 70*Y* of living material. The multinucleate protoplasm of the female thallus shown in figure 78 contains irregular vacuole-like spaces, similar to those described above, some of which seem to contain spherical bodies which have been interpreted as the stroma of fatty masses. These may be the bodies which Barrett (1912) described in the vacuoles of fixed and stained resting spores of *O. luxurians*. The nuclei of

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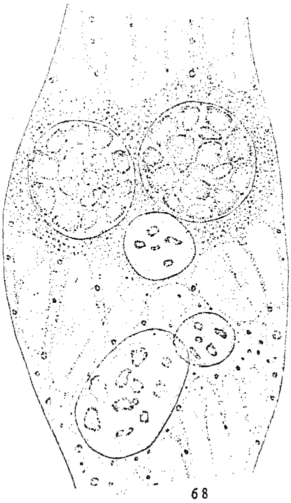
Explanation of figures 68–81.

FIGS. 68–72. Progressive stages in the development of an asexual resting spore (*X*) and a sexual resting spore (*Y*). × 630. FIG. 68. Female thalli containing large, irregular fatty masses; the male thallus is similar in appearance to the zoosporangial thalli near by. FIG. 69. The male thallus remains unchanged while the fatty masses in the female thalli *X* and *Y* have become smaller and more numerous; the thalli are surrounded by a hyaline layer. FIG. 70. The male thallus contains numerous small refringent masses while the female thalli contain dispersed, indistinct oil bodies; the host protoplasm has completely disappeared and the exospores have completely developed; the endospore of resting spore *X* is developing. FIG. 71. Resting spore *X* has a well formed endospore and is filled with homogeneous protoplasm in which spherical fatty masses are visible. The contents of the male thallus are in the process of moving into the female thallus *Y*. FIG. 72. Mature resting spores are with large, central refringent masses. FIG. 73. A young, multinucleate female thallus containing brightly staining bodies which have been associated with the refringent masses of living material. × 1130. FIG. 74. A multinucleate parthenogenetic resting spore of *O. Achlyae*; numerous granules of host protoplasm surround the margin of the exospore, which exhibits centripetal radial lines of deposition. × 1640. FIG. 75. Metaphase plate stages of division of nuclei in an asexual resting spore. × 1140. FIG. 76. An empty, germinated resting spore showing the exit tube. × 620. FIG. 77. A parthenogenetic resting spore showing unusually large nuclei with large chromatin masses. × 1640. FIGS. 78–79. Incipient sexual resting spores stained with Flemming's triple stain showing many nuclei in prophases of division. × 1640. FIG. 80. A sexual resting spore which was fixed just as the contents of the male thallus were moving into the female thallus. × 1140. FIG. 81. A mature asexual resting spore stained with Flemming's triple stain showing the multinucleate, homogeneous, peripheral layer of protoplasm surrounding the central fatty mass; the thallus possesses a smooth endospore and a rough exospore. × 1140.



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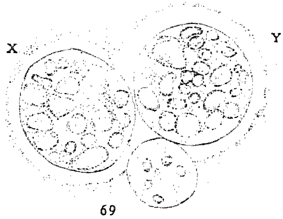

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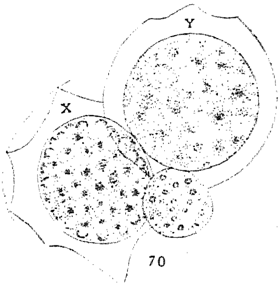

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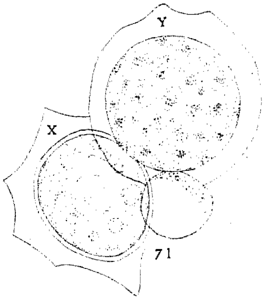

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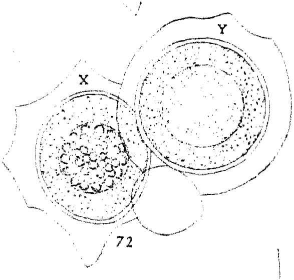

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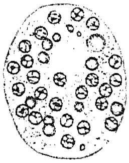

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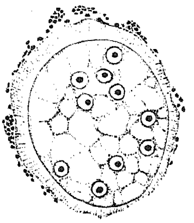

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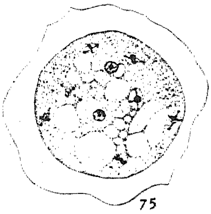

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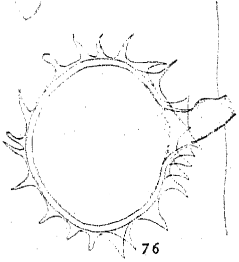

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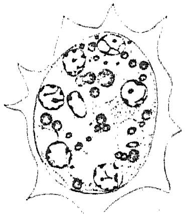

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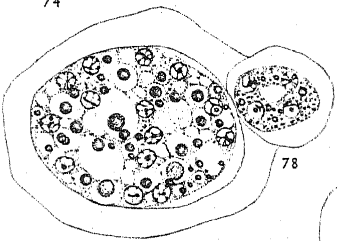

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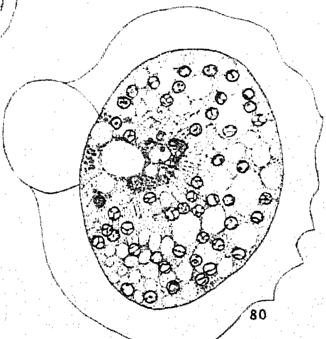

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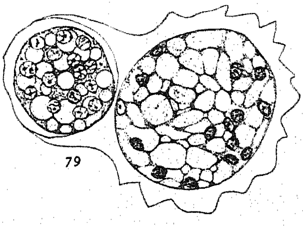

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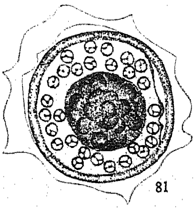

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both the male and the female thalli seem to be in the prophases of division. The content of the former, however, is badly shrunken. In figure 79 a very similar organization of the protoplasts is illustrated. Probably because of the difficulties involved in securing proper fixation of the female thalli after the deposition of the exospore, the nuclei are indistinct and poorly stained.

The passage of the contents of the smaller thallus into the larger is shown in figure 71*Y*. This process may be completed in a few minutes, although the passage of the male protoplast into the female cell may take several hours. There is little change in the appearance of the protoplasts, although in 71*X* the coalescence of the dispersed fatty material has begun in preparation for the formation of the central refringent mass of the mature spore.

Figure 80 represents a sexual resting spore which was apparently fixed while the contents of the male cell were still flowing into the female thallus. From the region of the "fertilization" pore, distinct radiations may be seen which suggest that there were lines of flow in the protoplasm when fixation occurred. As may be observed in figures 78 and 79, the nuclei of the male and female thalli are similar in appearance. Consequently, they are indistinguishable in this preparation. Several pairs of nuclei may be seen but such relative positions appear to be fortuitous. So far, the author has found no indication that the nuclei fuse in pairs as described by Barrett (1912) for *O. vexans*. In some resting spores unusually large nuclei, which at first might have been regarded as fusion nuclei, were observed. The subsequent discovery of such giant nuclei in asexual resting spores (fig. 77) as well as in zoosporangia (fig. 36) indicated, however, that these are merely artifacts.

At maturity, the peripheral region of the spore cavity is filled with homogeneously granular protoplasm with few if any refractive bodies. The center of the spore, however, is occupied by a single, spherical refringent body (fig. 72*Y*) or by an aggregation of many small globules (fig. 72*X*) which, when treated with Sudan III, gives a brilliant red reaction, indicating that it is composed of fatty material.

In figure 81, a fixed and stained median section of a mature, asexual resting spore of *O. Achlyae* is shown. The central area of the spore is occupied by the central body which, with Flemming's triple stain, appears reddish-purple. Surrounding this, in a layer of homogeneous protoplasm, are numerous well defined nuclei containing blue chromatin masses. The exospore and endospore, which have been separated by the microtome knife in the process of sectioning, are clearly distinguishable. The endospore shows a marked affinity for crystal violet, while the exospore fails to stain with haematoxylin and colors very slightly with orange G.

The resting spore, upon germination, becomes transformed directly into a sporangium and liberates zoospores by means of an exit tube (fig. 76) in a manner similar to that described by Shanor (1939) for *O. varians*. Very few germinating resting spores of *O. Achlyae* have been observed. Consequently, no detailed account of the process of germination can be given.

Host-Parasite Relationship. The penetration of the germ tube into the host protoplasm and the subsequent liberation of the parasitic thallus may cause a localized agitation of the host protoplasm. The refringent bodies of the host protoplasm often swirl in eddies around the young thallus (fig. 4) and obscure it from view. If this may be taken to indicate a distinct reaction between the parasite and the host it is indeed of short duration for, when the thalli next become visible in the filaments (figs. 16, 17), they appear similar to regular inclusions carried about in the streaming protoplasm of the host. A hyaline zone surrounding the parasite, such as Emmons (1931) describes for *Cicinnobolus,* has not been observed. No digestion spaces, described by Smith (1900), Rice (1934), Aronescu (1934), and others in relation to haustoria of *Erysiphe, Puccinia, Diplocarpon,* and other parasitic fungi, have been seen in any stage of development. Three young thalli, as they appear in fixed and stained material, are illustrated in figure 33. Resting nuclei of the host appear quite normal and may be seen in the immediate vicinity of the thalli. No division of the host nuclei in parasitized filaments has been observed, but as Couch (1932), Raper (1936), Wolf (1938), and others have shown, nuclear divisions seldom occur in the distal portions of oomycetous fungi. Consequently, this lack of division stages of the host nuclei is not to be regarded as a reaction to the presence of the parasite. Longitudinal striations in the *Achlya* protoplasm, similar to those illustrated by Hillegas (1940), plate 5, figure 71, indicate that streaming was in progress in the filament when fixation took place.

As the thalli increase in size, however, the ''free floating'' phase is terminated, and the thalli become relatively localized in the filaments (figs. 18, 19). At this time there is a marked tendency for the protoplasm from all parts of the filament to flow toward and accumulate around the parasites. At the same time hypertrophy of the filament, in the immediate vicinity of the thalli, usually becomes noticeable. As the swelling increases in size, vacuoles appear in the host protoplasm, and radially arranged cytoplasmic strands running from the thalli to the peripheral layer of host plasm may be seen. The granules of the host protoplasm continue to stream into the swollen region of the filament. This movement goes on until all of the visible contents of the entire host filament have been attracted to and absorbed by the developing thallus (fig. 22).

In some instances the swelling of the filament seemed to be initiated in the immediate vicinity of a thallus lying near the host wall (fig. 16). This, however, was by no means the general rule.

Infection with *O. Achlyae* does not invariably bring about an appreciable enlargement of the host filament. The development of sporangia within filaments containing limited amounts of visible protoplasm often occurs without showing the characteristic radial arrangement of the host protoplasm and without causing localized swelling of the filament. Furthermore, in the few infected *Achlya* oogonia which were observed, no swelling or distortion of the oogonial cell was detected. This evidence seems to indicate that the parasite does not cause the host cell to swell by direct stimulation. The parasite seems rather merely to induce the host protoplasm to flow toward it and to accumulate in its vicinity. Consequently, the induction and subsequent growth of the localized swellings appear to be correlated to some degree with the amount of dense protoplasm available in the parasitized filament. The similarities which exist between the formation of these pathological swellings and the development of incipient zoosporangia of *Achlya,* are rather suggestive. In the latter the protoplasm flows rapidly into the tip of the filament, which then swells to accommodate the increased volume. Septation occurs and the young sporangium is cut off from the "sporangiophore," which in turn is left almost devoid of optically differentiated protoplasm. In infection by *O. Achlyae*, the protoplasm of the *Achlya* filament is induced to flow from the more remote parts into the region occupied by the thalli. The filament, consequently, grows in diameter so as to increase its volume locally. No septation of the filament occurs. The walls of the swelling are composed of cellulose and approximate in thickness the walls of normal filaments. This suggests that, if the wall is stretched and becomes thinner as a consequence, this is compensated by a local deposition of new wall material. It can be shown by plasmolytic methods, however, that the wall of the filament is somewhat stretched in the region of such swellings (Diehl 1935).

When infection of an oogonial cell which has been delimited by a cross wall takes place, a clearly defined unit of host protoplasm is involved. The parasite, unable to attract quantities of protoplasm from other parts of the filament, is consequently unable to cause any enlargement of the oogonial cell. Similarly, parasites developing in filaments which contain limited amounts of protoplasm do so without bringing about any appreciable swelling of the host filament.

As mentioned above, the protoplasm of the host may become highly vacuolate in the vicinity of the thalli as the development of the swelling proceeds. Dufrenoy (1936) maintains that such vacuolization may be the result of an effort, on the part of the host cell, to revert to a condition suitable for active metabolism. Although Dufrenoy's interpretation seems to be compatible with the observations of the writer, a thorough physiological analysis must be undertaken before any authoritative statement can be made.

DISCUSSION

Sexual reproduction has now been reported in a large number of chytrid species, but the cytological details in many remain unknown. Resting spores may arise after planogamic fusions, or as a result of fusions between uninucleate or multinucleate male and female thalli which may take place by means of fertilization pores, or by the production of conjugation tubes. These various types of sexual reproduction, however, do not appear to be confined to any particular family or genus. In the Synchytriaceae planogamic fusions have been described in species of *Synchytrium* and *Micromyces* by Kusano (1930), Köhler (1930), and Couch (1931). Kusano and Köhler believe that sex in *S. fulgens* and *S. endobioticum* is purely relative. In species of the family Olpidiaceae, however, fusions between isogametes have been described by Kusano (1912, 1929) for *Olpidium Viciae* and *O. Trifolii* while fusions of uninucleate male and female thalli have been observed in *Monochytrium Stevensianum* and *Olpidium radicale* by Griggs (1910) and Schwartz and Cook (1928). Planogamic fusions of isogametes have been reported in various Rhizidiaceous species by Scherffel (1925), while Serbinow (1907) describes fusions between uninucleate male and female thalli by means of fertilization pores in *Sporophlyctis rosata*. In the majority of species in this family, however, the passage of the contents from the male into the female thallus takes place by means of a long conjugation canal similar to that which has been observed for *Zygorhizidium* (Lowenthal 1905), *Polyphagus* (Wager 1913), and others. In the Woroninaceae multinucleate male thalli of *Olpidiopsis* (Barrett 1912; McLarty 1941) fuse with multinucleate female thalli by means of a small pore which develops at the point of contact between the two thalli. A similar condition has been described for *Ectrogella* by Scherffel (1925), while in *Pythiella* fusion between thalli is accomplished by the production of a short conjugation tube (Couch 1935).

Almost without exception, sexuality in chytrid species in general does not seem to be fixed and definite. In most species which have been critically examined from the stand-point of sexual reproduction, no evidence of genotypic differentiation of sex has been advanced. In *Olpidium Trifolii*, however, Kusano believes that planogamic fusions occur only between motile cells from different sporangia. Couch (1939) reports heterothallism in *Rhizophlyctis rosea* and *Pringsheimiella dioica*, but no detailed observations have, as yet, been published.

It has been shown by the author (1941) that in *Olpidiopsis Achlyae* genotypic sexual differentiation does not occur. As Barrett (1912) observed for species of this genus which he studied, the male and female thalli appear to be essentially similar to the zoosporangia, differing from the latter mainly in the elaboration and disposition of fatty material throughout the later stages of their development. Plasmogamy occurs in *O. Achlyae* between multinucleate thalli. No nuclear degenerations similar to those described in the sexual processes of many of the higher Oomycetes have been observed in *O. Achlyae*. Barrett observed what he believed to be stages in the fusion of nuclei in resting spores of *Olpidiopsis vexans*. No indications of karyogamy in *O. Achlyae*, however, have been encountered. In this species, which produces sexual or asexual resting spores, it has been found that "fertilization" is in no way essential to the maturation of the female thalli. At maturity, both sexual and asexual resting spores of *O. Achlyae* are multinucleate and in germination the spores function directly as zoosporangia. In this regard they differ from the uninucleate resting spores of *Polyphagus Euglenae* (Wager 1913), and *Endochytrium operculatum* (Hillegas 1940).

Atkinson (1909) considers that the passage of the entire contents of the male thallus into the larger female cell through a pore without any indication of an antheridial tube indicates that this is a primitive type of sexuality rather than a reduced or degenerated form. The multinucleate condition of the fusion thalli, likewise, has been considered primitive by some observers. Similarly the series from multiple nuclear fusions in *Albugo Bliti* to fusions between single pairs of nuclei in *A. candida* has been considered as exemplifying within a single genus the evolution which has gone on from coenogamic fusions toward the condition which is commonly found in the higher oomycetes. In our present state of knowedge, however, true sexuality may or may not exist in species of *Olpidiopsis*. Until karyogamy is definitely demonstrated in the formation of sexual resting spores of this genus we can do no more than speculate on the relationships between *Olpidiopsis* and the higher fungi.

SUMMARY

The infection of the host by the zoospore of *Olpidiopsis Achlyae* is accomplished by means of a delicate penetration tube. Each uninucleate protoplast thus introduced develops independently into a multinucleate thallus.

Cytokinesis within mature multinucleate zoosporangia is carried out by centripetal cleavage furrows which develop progressively from one or more centrally placed vacuoles. Biflagellate zoospores emerge fully formed from one or more exit tubes.

Nuclear division in *Olpidiopsis Achlyae* is mitotic and simultaneous. The large nucleolus seems to function in the elaboration of the chromosomes. Although central bodies are present at the poles of the intra-nuclear spindle, distinct astral radiations are seldom visible. The chromosome number is six. Meiotic division has not been observed.

The early developmental stages of the resting spore are similar to those of the zoosporangium. Subsequently, however, the resting spore thallus distinguishes itself by the elaboration of large quantities of fatty material. At maturity the resting spore contains a large centrally placed refringent body surrounded by a multinucleate layer of slightly granular protoplasm.

Before the development of the resting spore of *Olpidiopsis Achlyae* fusions between two or more multinucleate thalli may occur. Karyogamy, however, has not been observed.

At maturity, the resting spore functions as a zoosporangium, liberating zoospores directly by means of an exit tube.

The thalli of *Olpidiopsis Achlyae* seem capable of attracting and subsequently absorbing the protoplasm of the entire infected filament. The swelling of the host cell, which usually occurs in the immediate vicinity of the parasite, seems to develop as a result of this local accumulation of excess host protoplasm rather than in response to a direct stimulation of the host by the parasite.

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STUDIES IN THE ERICALES. A DISCUSSION OF THE GENUS BEFARIA IN NORTH AMERICA

W. H. Camp

INTRODUCTION

Befaria,[1] like many woody genera present in North America, has its greatest accumulation of species in South America. In consequence, one hesitates to undertake a critical study of the North American forms without having first solved the complexities of the genus as it occurs in South America. Owing to present world conditions and the concomitant difficulties of travel and specimen exchange, various critical collections cannot be examined, which forces postponement of the nomenclatural phase of the problem as it relates to the South American members of the genus. However, sufficient specimens are at hand to enable one to arrive at some conclusion about the morphological archetypes of the group as well as their distribution. Therefore, in order to understand those of our own species which are taxonomically troublesome, an attempt is here made to fit them into the species-pattern of the ancestral forms entering the area. While this procedure does not make the identification of any particular specimen any easier, it does bring to our study a certain perspective not otherwise obtained.

It is evident that the genus *Befaria* has not, in some characters, advanced nearly so far as others of the Ericaceae; that, while it is not to be thought of as ancestral to its relatives, it yet retains certain of the floral sructures which must have been characteristic of the primitive Ericalean type. In addition to discrete rather than fused corolla segments, the character perhaps most indicative of a retained primitive condition is the often variable number of flower parts in each cycle, this in itself being an indication that the basic genetic pattern is neither rigidly controlled nor highly evolved. A further indication of primitiveness is the presence, in many species, of a glandular pubescence on various plant organs, a feature common to the majority of the more primitive members of various groups of the Ericales.

It would appear that during the Early Tertiary or perhaps even the latter part of the Cretaceous the genus had much the same general distribution as today, but it is probable that the number of species was considerably less than that recognized in the most recent monograph.[2] It is also apparent that both during and subsequent to the various orogenic and subsidence cycles of the Middle and Late Tertiary the distributions of various basic species of the genus were disorganized.

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[1] The question as to whether the spelling should be *Befaria* or *Bejaria* is not taken up here; it is of no importance in the present discussion, the two being considered only variant spellings of the same name. For those interested in such matters, reference may be made to Small, N. Am. Flora **29**: 35. 1914 (*Befaria*); Fedtschenko and Basilevskaja, Bot. Gaz. **85**: 299. 1928 (*Bejaria*); Sprague, Kew Bull. **1928**: 347. 1928 (*Bejaria*); Mansfeld and Sleumer, Notizbl. **12**: 242. 1935 (*Befaria*); as well as the earlier writers cited by these authors.

[2] Mansfeld, R. & Sleumer, H. Revision der Gattung *Befaria* Mutis. Notizbl. **12**: 235–276. 1935.

BEFARIA IN THE UNITED STATES

In a genus where specific lines are often difficult to determine, the lack of individual variability is perhaps the most striking feature of *B. racemosa* Vent., a species fairly abundant throughout much of Florida, with casual outliers in Georgia and a single specimen (doubtful) from "Mobile" [Alabama?] (*Cozzens* in 1826). In fact, the specimens are so nearly similar that one might suspect that they all came from the same clone.

The stable condition of *B. racemosa* is probably due to its long isolation from any other of the Befarian stocks. Only recently have students of the flora of the southeastern coastal plain of the United States realized that a portion of Florida has been emergent since at least the Oligocene. It is becoming continually more obvious that this island, for a considerable length of time isolated from both the mainland to the north and the main mass of Antillia (but connected with this latter mass during the Early Tertiary), has played an important rôle in the composition of our present-day southeastern coastal plain flora.

Prior to the Oligocene the exact story of this relatively small bit of land is obscure but, being connected with the western portion of Antillia probably during at least the latter part of the Cretaceous, this area (now part of Florida) was one into which the early tropical and subtropical lowland floras could migrate. From the Oligocene until the late Pliocene, or even the Pleistocene, it was an island separated from the mainland of North America by several hundreds of miles of open ocean. Thus, lying on the outer fringe of the primary Befarian dispersal and, from at least the Oligocene to the Pleistocene having been isolated on a comparatively small island, it is only natural that *Befaria racemosa* should be practically homozygous and therefore morphologically stable.

BEFARIA IN THE CARIBBEAN

Throughout at least part of the Tertiary, Antillia was joined with both South America and Central America. But this great land mass, with its east-west-trending ranges of mountains, was on the outer fringes of the distribution of *Befaria* and, as a result, held only a small segment of the genus. Today, we know only one species from the interior of the Antillean area, *Befaria cubensis* Griseb., from western Cuba. However, it is possible that subsequent exploration on the higher peaks of Oriente in Cuba, or even in Hispañola, may uncover material as yet unknown to us. *B. cubensis*, although today a distinct and reasonably stable species, is reminiscent of the

Venezuelan and Colombian *B. ledifolia* H. & B., and seems to have had genetic connection with it in the past. It is also possible that the tendency for revolute leaves in many of the South American forms may have been derived from this segment of the older Befarian complex.

THE PROBLEM IN BEFARIA

If we now turn our attention to the bulk of the known Mexican species and those southward into South America, no such stability of morphological characters is to be noted as was found in *B. racemosa*. Nevertheless, if we are ultimately to understand the genus, if we are to rationalize our present nomenclatural system with the fundamental biology of the group, we must first arrive at a rather definite concept of its primitive biotypes as well as their distribution. It is to be admitted that, for the present, a complete picture of the genus is impossible, simply because certain critical areas are in need of considerable exploration. Nor am I as yet ready to commit myself in a definitive manner concerning the exact pattern of speciation within the South American portion of the genus.

However, it is apparent that there have been several evolutionary trends in *Befaria*. One was a reduction of the more primitive, loosely flowered, racemose-paniculate type of inflorescence to a more compact and congested inflorescence. Others are the loss of the primitive type of Ericalean pubescence which resulted in a glabrous plant, and the introduction of revolute margined leaves. These evolutionary trends appear to be completely independent of each other. From this standpoint, it would seem that, after their earlier partial stabilization, the primary species-populations have, in certain areas, been mixed. This has resulted in a series of hybrid swarms of comparatively recent origin; complex populations of plants, the individuals of which apparently defy arbitrary placement in traditional taxonomic categories.

THE ARCHETYPES OF THE MEXICAN UPLANDS

Of the Mexican species of *Befaria* here recognized, only two seem to be representatives of an early dispersal.[3] The remaining appear to be of more recent origin.

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[3] It is possible that an additional species may yet be collected in Mexico, and attention should be called to the following: In December, 1936, I traveled from Veracruz to Oaxaca by way of Orizaba. Before the mountains were reached and while yet in the *tierra caliente* of the State of Vera Cruz, the train passed through a few inland swamps wherein some shrub with conspicuous flowers was occasionally seen. In one of these areas the train was traveling rather slowly and I was able to note the habit of the plants growing nearby. This shrub apparently was a species of *Befaria.* Unfortunately, I was unable to visit this area on my return in 1937; neither have I seen specimens from this region nor, so far as I can learn, have any been collected. These plants most certainly were not *B. mexicana,* having, if my memory can be trusted, an inflorescence somewhat intermediate between the paniculate type of *B. glauca* and the racemose appearance of *B. racemosa.*

Of these basic species,[4] the first to be considered is *Befaria mexicana* Benth. This species ranges in Mexico from Durango [?] (*Seemann 2130* is so listed by Mansfeld and Sleumer) and Zacatecas (*Hartweg 92*, type collection) southward and eastward through the Sierra Madre of Jalisco (*Mexia 1840*) and Guerrero (*Mexia 8956; Hinton 14106, 14200, 9935*, this last in Herb. Field Mus.) to Oaxaca (*Conzatti 2530*, N. Y. and Herb. Field Mus., *4355;* and *Schultes & Reko 939.*) Material from the northwestern part of the range apparently has larger corollas (± 3 cm. long) and is more consistently pubescent than that in Oaxaca, being thus closer to the typical form.

The other primary type with which we are concerned in Mexico is the material which has been formerly referred to *Befaria laevis* Benth. In their recent study, Mansfeld and Sleumer (l.c.) have noted that the Mexican *B. laevis* and the South American *B. glauca* H. & B. var. *typica* Mansf. & Sleum. are difficult to distinguish. In addition, they admit that the primary character (the leaf apex) which they use to separate these species is not reliable. I would go even farther and say that I am unable to differentiate the genetically uncontaminated Venezuelan and Mexican material of these two species. Consequently, I am led to the conclusion that the Mexican material, by previous authors placed in *B. laevis* Benth. (1840), should be transferred to the earlier *B. glauca* H. & B. (1809).

It might, naturally, be argued that a species should not have so disjunct a distribution, but it is well to recall that (even among the Ericaceae) *Befaria* is an old genus and that much of the area of its early distribution has been subject to extensive diastrophic activity and consequent floristic disturbances. Therefore, it is altogether likely that *B. glauca* has been lost from parts of the area where it once grew.

If we examine the known distribution of *B. glauca* in Mexico (*B. laevis* of previous writers) we find that it extends from Chiapas (*Purpus 10285; Matuda 2589*) into Oaxaca (*Hartweg 478*, type coll. of *B. laevis; Ghiesbreght 31*, type coll. of *B. Ghiesbreghtiana;* and *Schultes 677*). Mansfeld and Sleumer (l.c.) list additional specimens from Guerrero and Hidalgo, but *Schultze 468*, the one cited by them as from Guerrero, with white flowers

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Occurring as they do in the lowlands rather than in the mountains, the identity of these plants remains an interesting problem, the solution of which may shed considerable light on the early northward dispersal of this genus, for these same lowlands are phytogeographically connected with the western parts of ancient Antillia. In this connection, it is well to remember that, although the genus consists mainly of mountain forms, *B. cubensis* and *B. racemosa* are found only near sea-level.

[4] Unless otherwise noted, the specimens here cited are in the Britton Herbarium of the New York Botanical Garden. I also wish to thank the Curators of various American herbaria who made a fruitless search for certain specimens, and particularly Mr. P. C. Standley of the Field Museum for his kindness in submitting a series of unusually interesting collections.

and petals 3 cm. long certainly cannot be *B. glauca* (or *B. laevis*) in its pure phase. Of the two "Hidalgo" specimens cited by them I have before me *Ghiesbreght 31*, which was not from this state but from Oaxaca;[5] the other (*Seler 866*) I have not seen. I also have before me (without locality) *Sessé, Mocino, Castillo* et *Maldonado 1813* (Herb. Field Mus.). It is obviously conspecific with the others placed here in *B. glauca*.

Before we continue with our analysis of the Mexican species of *Befaria*, it will be advisable first to examine material of these two basic species from areas where it would appear that they have not been subject to interspecific contaminations. Briefly, in Chiapas we find that *B. glauca* has glabrous leaves, glabrous branches, a coarse paniculate inflorescence which, also, except for a minute and early deciduous puberulence, is glabrous. The petals are 1–1.5 cm. long and of a deep pink or rose color. Paler forms and those with larger corollas sometimes found in other regions apparently have a mixed heredity.

Conversely, in Zacatecas, Jalisco, and parts of Guerrero, *B. mexicana* has the leaves glandular pubescent on both surfaces, particularly along the midvein below. The branches are densely glandular pubescent as is the inflorescence which, in contrast to *B. glauca*, is compact and subcorymbose. The petals are 2.5–4 cm. long and white, although pink forms are occasionally recorded. These, in my opinion, may be due to a slight contamination of *B. glauca* heredity. *Mexia 1840* from Jalisco is in fruit.

These very distinct forms seem to represent the two original species present on the Mexican uplands.

THE BEFARIA DISCOLOR COMPLEX

Turning our attention to a region where *Befaria glauca* and *B. mexicana* come together, we are confronted with the following situation: a complex population generally placed in *B. discolor* Benth., but possessing combinatory and segregate forms apparently derived by hybridization from both species. Certain examples, all from the State of Oaxaca, are here briefly analyzed.

Conzatti 2529 (Herb. Field Mus.) with its dense pubescence and petals ± 2.5 cm. long would, in spite of the short corolla, be nearly typical *B. mexicana*, except that the dried plant retains evidence of considerable color in the flower. This number is of particular interest in connection with the previously cited *Conzatti 2530* (collected in the same locality, on the same date), with an apparently white corolla and petals 3–4 cm. long, which was placed in *B. mexicana*.

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[5] Mansfeld and Sleumer (l. c.) list *Ghiesbreght 31* from Hidalgo. However, the specimen on deposit at the New York Botanical Garden clearly states that this number was collected in Oaxaca, as does the original description of *B. Ghiesbreghtiana* Fedtschenko & Basilevskaja, Notul. Syst. Herb. Hort. Bot. U.S.S.R. **6**: 38. 1926.

Liebmann 8592 (Herb. Field Mus.) has the branches and inflorescence as pubescent as any specimen of *B. mexicana* that I have seen, yet its corolla was apparently deeply colored; also, the petals are only 2–2.5 cm. long.

The pubescence of *Mexia 9276* is, again, nearly typical for *B. mexicana*, yet the inflorescence form is that of *B. glauca;* the petals are white, but only ± 2 cm. long.

Galeotti 1812 (type coll. of *B. floribunda* Mart. & Gal.) has the branches pubescent, but the pubescence becomes sparse in the inflorescence, with the upper part of the pedicels and calyces completely devoid of the glandular setae so characteristic of *B. mexicana.* The inflorescence resembles that of *B. glauca,* but its individual branches are compacted, much as in typical material of *B. mexicana.* It would appear that the petals were not more than 2 cm. long. The original description states that the flowers are "purpureo-albis"; the field notes list the color as "rosees."

Gómez & Gómez 6000 has almost completely glabrous leaves,[6] the branches are pubescent, but the setae on the pedicels are even more reduced than in the previously cited *Galeotti 1812,* a few flowers having a completely glabrous calyx and only a few scattered hairs on the pedicel. The corolla is ± 2 cm. long and a deep rose-pink color.

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[6] *Manuel Gómez & Victoria Conzatti de Gómez* (Herb. Conzatti) *6000* from the District of Teotitlan, Oaxaca, was kindly loaned to me by Richard Evans Schultes, who received it from Professor Conzatti. This collection (the portion studied now deposited in the Economic Herbarium of the Harvard Bot. Mus.) is of particular interest because it is the basis of a new monotypic genus—*Heptacarpus*—(Conzatti, Prof. C. Organo Transitorio en una Talamiflora Serrana. Anal. Hospital Gen. Oaxaca **2**: 4–7. *1 plate.* 1940.). This genus, according to the present International Rules of Botanical Nomenclature, is invalidly published (being without Latin diagnosis); it is also incorrectly placed as to family.

The following personal communication from Mr. Schultes is pertinent to the present discussion and is included:

"In 1839, Hartweg collected the type of *Befaria discolor* at Talea de Castro (Long. 96° 17′, Lat. 17° 21′), District of Villa Alta in northeastern Oaxaca, only a few miles southeast of the locality of collection of *Gómez & Gómez 6000.*

"In the same year, Galeotti made a collection which became the type of *Bejaria floribunda* Mart. & Gal. (=*Befaria discolor* Benth.). This collection (*Galeotti 1812*) was made on the mountains near San Ildefonso Villa Alta (Long. 96° 10′, Lat. 17° 21′) and San Juan Tanetze (Long 96° 19′, Lat. 17° 23′). Villa Alta is slightly east of Talea; Tanetze is but several miles east of Cacalotepec and slightly west of Talea. The specimen in the Gray Herbarium is labelled as coming from the "Chinantla," a name which Galeotti used to designate the mountainous areas of the Districts of Villa Alta and Choapam.

"A third collection was made by Jurgensen in the Sierra San Pedro Nolasco near Talea de Castro. This collection (*Jurgensen 562*) became the type of a new genus—*Jurgensenia*—and species—*J. mexicana* Turczaminov (=*Befaria discolor*).

"These collections, all made within a radius of fifteen miles, have been the basis of material described and placed in two different families—Ericaceae and Theaceae; three genera—*Befaria* (*Bejaria*), *Jurgensenia,* and *Heptacarpus;* and four species—*Befaria discolor, Bejaria floribunda, Jurgensenia mexicana,* and *Heptacarpus salmonicolor,* thus adding to the confusion surrounding *Befaria discolor* Benth."

Hartweg 479 (type coll. of *B. discolor* Benth.) has essentially glabrous leaves, or with a few gland-hairs on the midvein below; the stem has a sparse pubescence, and the pedicels even less. The inflorscence is but little branched, as is common in *B. mexicana*, but it is loose-flowered with spreading pedicels, and thus is much more like that of a single branch of the *B. glauca* type. The calyces are glabrous and the petals 1.5–2 cm. long.

Apparently, then, *B. glauca*, coming from the east, perhaps by way of uplands now submerged, met the Mexican representatives of the *B. mexicana* population and, in the Oaxacan region, produced a series of rather complex hybrid forms. The presence of nearly pure stocks of both species in Oaxaca, as well as these intermediates (today apparently concentrated in the region of the "Chinantla"), indicate that such a sequence of events has taken place.

Our problem, then, is to determine just how we shall treat such a situation. In Mexico, owing to the present isolation of the more mesophytic floras on mountain ranges, or even individual peaks, and these often separated by wide expanses of semi-desert, a considerable amount of endemism is to be expected. With further exploration and a larger series of critically collected specimens, it would not be surprising to learn that certain of these segregates, carrying combinatory characters of both the basic species, have become genetically stabilized and exhibit a reasonably constant set of morphological characters within restricted areas.

For the present, and until we know more concerning them, I see no need to make the problem taxonomically more complex by resorting to a formal description of all of these segregate and morphologically different individuals, thus multiplying our nomenclatural troubles. Instead, it is my suggestion that we consider this problem from the standpoint of expediency; that we do not consider *Befaria discolor* Benth. a true biological species having had a single origin; rather, that it be only a nomenclatural convenience —a name applied to those individuals which, *in sensu stricto*, cannot be placed either in *B. mexicana* or *B. glauca* but would appear to be recurrent segregates of hybrids resulting from crosses between these two species.

A study of the Central American and South American material of *Befaria* indicates that much the same situation exists there as in Mexico involving *B. glauca* and additional species present in the area. Consequently, it is my opinion that Mansfeld and Sleumer (l.c.) have not solved the obviously difficult systematic problem encircling *Befaria* by a traditional taxonomic treatment. This is nowhere better shown than in their disposal of the South American forms allied to *B. glauca*, in which they described four new varieties under this species in addition to the typical form; varieties with monotonously similar distributions and which, when critically examined, clearly indicate hybrid connections with other (and I think valid) species recognized by them from within the same area. I believe that, if they could be crossed and the resultant hybrids were fertile (which from the material available seems to be the case), one could start with but four of our modern species, *B. ledifolia*, *B. glauca*, *B. Mathewsii*, and *B. mexicana* and, in only a comparatively few generations of plants, produce segregate forms indistinguishable from the majority of the species and varieties now recognized in South America. This does not mean that the bulk of these forms are necessarily of recent hybrid origin—although many of them are—but only that, in taxonomic work, one should attempt to distinguish between those which appear to be genetically stable and those which have been given taxonomic rank and placed in the same category merely because of simulative characters—similar forms which are the result of a series of chance segregations from within a hybrid complex. Such so-called "species" are met with all too frequently in the Ericales in such genera as *Befaria*, *Rhododendron*, *Gaultheria*, *Pernettya*, and *Vaccinium*.

However, one cannot leave this problem of the hybrid origin of the Mexican complex, here covered by the name *Befaria discolor*, without certain additional remarks. It is interesting to note that, typically, *B. mexicana* is a "winter bloomer," being in flower from November until late in March, a span of more than four months. Conversely, *B. glauca* is a "summer bloomer," the specimens before me indicating that flowers are present from May into August. It is to be further noted that those specimens placed by me in *B. discolor* span the season of both the other species, flowering plants being recorded at various times from November to June.

It is, of course, well understood that in the tropical uplands the seasonal distribution of rainfall plays an important rôle in the flowering of a majority of species. My own experiences indicate that this is certainly true in the Oaxacan region. However, since there is no great change in the seasonal temperatures, it is not unusual for individual plants to be thrown completely out of their normal flowering period by other factors. Among these may be mentioned unseasonal distributions of rainfall, flower-bud production on the new growth following insect injury and, particularly, the flowering of sprouts after fire. It is to be pointed out in this connection that nowhere in Mexico is the *milpa* type of agriculture more intensively developed than in the mountainous regions of Oaxaca. The burning of these small areas often starts extensive brush fires and, in 1937, to the east of Villa Alta (see footnote 6) on the border of the "Chinantla," while standing in one of these recently burned-over areas, I could see the smoke of at least three such fires on adjoining mountains. Furthermore, this is not a new type of agriculture in the region, having been practiced there for untold centuries.

Therefore, it is probable, although *B. mexicana* and *B. glauca* normally have different flowering periods, that abnormal conditions of one sort or another have induced individual plants of either species to close the short gap in flowering seasons, thus permitting a mixing of the two species' heredities. It is also evident that such a condition is not limited to the past, but is going on actively at the present time so that, today, we must recognize the presence of current hybrids between these two species as well as a series of segregates from those of the past. It is because of this that I look upon the type of *Befaria discolor* Benth. not as representative of a true biological species but, rather, as only one of a group of divergent forms of complex origin, having in common only a basic bispecific ancestry.

A NEW SPECIES FROM MEXICO

In a previous paragraph I have intimated that it is possible, in certain areas contiguous to the Oaxacan region, that future exploration may uncover populations of individuals, probably of segregate origin, but sufficiently stabilized so that they may be dealt with in a more particular manner. Such entities, while not a part of the ancestral population, might well be thought of as true species—ones which have had their origin in relatively modern times.

I have before me a specimen representative of a group which seems to belong in such a category. It was collected by Mr. Geo. B. Hinton in Guerrero, away from the immediate influence of *B. glauca* and in a region where *B. mexicana* is the dominant form. The collection is from a tree 6 meters tall and, from the material at hand, it would appear that the vegetative parts almost exactly duplicate those of *B. glauca*, although the flowers simulate those of *B. mexicana*, the petals being white and up to 4.5 cm. long. It is also of interest to note that, under *B. laevis* (*B. glauca* of this paper), Mansfeld and Sleumer (l.c.) mention a similar specimen, also from Guerrero (*L. Schultze* Jena *n. 468*), with large flowers, the petals being white and 3 cm. long. I therefore propose the following new species:

Befaria Hintonii Camp, sp. nov. Arbuscula 6 m. alta, ramulis glabris; folia oblongo-lanceolata, utrinque glabra, apice acuta, supra subnitida, subtus glaucescentia, 5–8 cm. longa, 1.5–2.5 cm. lata; inflorescentiae breviter racemosae vel subcorymbosae, 6–12-florae; rhachis pedicellique glabri, pedicellis crassis, 3–4 cm. longis, bracteis parvis deciduis; calyx campanulatus glaberrimus, sub anthesi circ. 8 mm. latu, lobis ovatis obtusis, margine ciliatis; petala alba, obovata-spathulata, basi attenuata, 4–4.5 cm. longa, circ. 1 cm. lata, apice extremo parce puberula; stamina petalis aequilonga; stylus tenuis circ. 5 cm. longus.

MEXICO—GUERRERO: Dist. of Galena, Piedra Ancha, 2800 m., *Geo. B. Hinton 14237*, May 3, 1939. "Oak and pine forest; tree 6 m. high; flower snow white." TYPE in Herbarium of the New York Botanical Garden.

NOMENCLATURAL CHANGES

Befaria glauca Humb. et Bonpl. in Pl. Aequin **2**: 118, t. 117. 1809. Syn. *Befaria laevis* Benth., Pl. Hartweg., p. 65. 1840.

This change enlarges the distribution of the fundamental and once widespread *B. glauca* from South America into Mexico, the genetically uncontaminated Mexican material being scarcely distinguishable from the typical form in Venezuela.

×**Befaria discolor** Benth., stat. emend. Camp. [*Befaria mexicana* Benth. × *B. glauca* H. & B.] *Befaria discolor* Benth. Pl. Hartweg. p. 65. 1840. Syn.: *Heptacarpus salmonicolor* Conzatti, Anal. Hospit. Gen. Oaxaca **2**: 5. 1940. For additional synonyms see Mansfeld & Sleumer (l.c.)

The transfer of *B. discolor* from the status of a true species to that of a name covering a complex series of hybrids and their segregates has been undertaken solely in an attempt to rationalize our present system of nomenclature with what appears to be the biological situation within the material here under discussion. Any other procedure under the existing system would necessitate the giving of some sort of taxonomic standing to the group of names which necessarily would have to be attached to the known morphologically different and describable entities in the complex *Befaria*-population which appears to center in the mountains of northeastern Oaxaca. To do so at the present time would add nothing to our knowledge of the genus and certainly would not clarify its taxonomy.

BEFARIA IN CENTRAL AMERICA

It is of more than passing interest to note that no previous study of the genus has listed *Befaria* from Central America. Fortunately, my attention has been called to four collections from this region recently deposited in the Herbarium of the Field Museum; one from Honduras and three from Guatemala. A genus with such showy flowers is not easily missed by collectors. That it was neither found in Honduras prior to 1936, nor in Gautemala earlier than 1939 indicates either that *Befaria* is exceedingly rare in Central America, or (as I suspect) that the area is in need of considerably more botanical exploration.

These four specimens show some relationship with the Mexican populations, but, owing to certain differences, I am unable to place them in any of these species with confidence.

The single specimen from Honduras (*Yuncker, Dawson & Youse 5823*, July 13, 1936, from a steep ravine near El Achote, hills above the plains of Siguatepeque, Dept. of Comayagua), because of its viscid pubescence, seems to be related to *Befaria mexicana*. However, the leaves are somewhat larger (being up to 10 cm. long) and less glaucous than is typical; the inflorescence is considerably more loose; the pedicels are attenuate, and the calyces only one-half to one-third the diameter they should be for this species. The petals are white and at most 2.5 cm. long, being, thus, just within the lower limit for *B. mexicana*. Although tentatively placed in association with this species, it is not to be thought of as typical.

The three specimens from Guatemala were collected in the Sierra de las Minas, Dept. of Zacapa, in October, 1939. Of these, two (*Steyermark 29775 & 29783*) were from an elevation of 1700–2000 meters. *Steyermark 29783* is in flower and with immature fruit. It was a "tree 30 ft. tall." The plant is glabrous and, in their shape, the leaves closely resemble those of *B. glauca* in its typical phase. The inflorescences are few flowered, the pedicels short and heavy, the calyces fairly large and the flowers white, sweet scented, with petals 2–2.5 cm. long; thus, in these characters it somewhat resembles *B. mexicana*. *Steyermark 29775*, in fruit, has much the same general appearance, but it is recorded as being a "shrub."

The third specimen, *Steyermark 29725*, from a lower elevation (1000–1500 m.), is a "tree 25 ft. tall." The plant is glabrous; the inflorescence is somewhat more diffuse than in the two previously cited specimens; the pedicels and calyces seem to be intermediate in form between those of *B. mexicana* and *B. glauca;* also, the flowers are small, being only 1.5–2 cm. long. The collector has made no note of the flower color, but in the dried specimen the petals are considerably darker than those of his #*29783*. It is probable that, when fresh, they were pink or even red; #*29725*, therefore, seems more closely to resemble *B. glauca* than the other Guatemalan specimens here cited.

In spite of their differences, one character in particular seems to be present in both the Honduran and Guatemalan specimens which, collectively, separates them from those species of the genus to which they might be referred. In general, the lower surface of the leaves of the various species of *Befaria* is definitely glaucous. This is not true of the Central American material available for, although the lower surface of the leaves is paler than the upper, it certainly is not glaucous, at least not in a degree characteristic of those species with which I have acquaintance.

On the basis of *Yuncker, Dawson & Youse 5823* from Honduras, I am predicting that *Befaria mexicana*, or its simulative counterpart, will yet be found in Central America. Also, I am certain that *B. glauca* in its pure form will be collected in Guatemala. This conclusion is reached after an examination of *Steyermark 29725* in conjunction with the distribution of *B. glauca* as here redefined, as well as its known presence in adjoining Chiapas. The remaining material from Guatemala apparently represents a new species.

Befaria guatemalensis Camp, sp. nov. Arbuscula 9 m. alta, ramulis glabris; folia oblongo-lanceolata, utrinque glabra, apice acuta, supra virida, subtus pallida non glaucescentia 5–9 cm. longa, 1.5–2.5 cm. lata; inflorescentiae breviter racemosae vel subcorymbosae 6–10 florae; rhachis pedicellique glabri, pedicellis sub-crassis, 1–3 cm. longis, bracteis parvis deciduis; calyx campanulatus glaberrima, sub anthesi circ. 4 mm. latu, lobis deltoidis, margine ciliatis; petala alba, obovata-spathulata, basi attenuata, 2–2.5 cm.

longa, circ. 0.5 cm. lata, apice extremo parce puberula; stamina petalis aequilonga; stylus tenuis, circ. 3 cm. longus.

GUATEMALA—ZACAPA: pine forest, Sierra de las Minas, near summit of ridge, below Finca Alejandria, alt. 1700–2000 m. *Julian A. Steyermark 29783*, Oct. 12, 1939. "Tree 30 ft. tall. Petals white, sweet-scented." TYPE in the Herbarium of the Field Museum. IBID: *Steyermark 29775*, said to be a shrub and with slightly larger leaves, may be only a sprout form of this species.

Befaria guatemalensis may be easily differentiated from the previously described *B. Hintonii* by its smaller flowers and pale green rather than glaucous lower leaf surfaces.

For the present, and until more material is available, no definite names are assigned to the single specimen from Honduras and the remaining collection from Guatemala, both of which are here suggested to be of possible hybrid origin between *B. guatemalensis* and the several other species probably present, but as yet uncollected, in the region. Further exploration, not only in Central America but also in the botanically little known Sierra Madre del Sur of Oaxaca and Chiapas, will be needed to shed light on the early northward dispersal of *Befaria* in the Americas as well as furnish us with additional clues useful in unraveling the tangled pattern of speciation within the genus.

KEY TO THE KNOWN MEXICAN AND CENTRAL AMERICAN SPECIES OF BEFARIA

- Plants essentially glabrous.
  - Flowers white.
    - Leaves glaucous below, petals 3–4.5 cm. long .... *B. Hintonii.*
    - Leaves pale, but not glaucous below; petals 2–2.5 cm. long .... *B. guatemalensis.*
  - Flowers pink or red, petals 1–1.5–(2) cm. long .... *B. glauca.*
- Plants with a glandular pubescence.
  - Upper part of inflorescence and calyces densely pubescent.
    - Flowers white, petals 2–4 cm. long .... *B. mexicana.*
    - Flowers pink or red, petals 1–2.5 cm. long .... ×*B. discolor.*
  - Upper part of inflorescence and calyces sparsely pubescent or glabrous, if glabrous, then the lower part of the inflorescence or branches sparsely pubescent; flowers predominately red or pink, or occasionally white, petals 1–2.5 cm. long .... ×*B. discolor.*

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THE BIOLOGY OF POLYPORUS BASILARIS

HAROLD E. BAILEY

(WITH FOUR FIGURES)

A brown pocket rot of *Cupressus macrocarpa* Hartweg has been known in California for a long time. Sporophores associated with this rot have been reported in Golden Gate Park, San Francisco, by workers in the Division of Forest Pathology, of the Bureau of Plant Industry, but, so far as the writer is aware, no detailed study nor description has been reported. The first material preserved for study was collected by Mr. H. E. Parks in 1923 on the Berkeley Campus of the University of California. Somewhat later, additional material from the same location was collected by Dr. Lee Bonar. These specimens, with study notes, were sent by Dr. Bonar to Professor L. O. Overholts, who made a study of the material. Having concluded that the fungus was an undescribed species, Overholts (in litt.) has proposed the name, *Polyporus basilaris* sp. nov. and characterized it as follows:

Polyporus basilaris Overholts sp. nov. Sporophora annua vel incremento marginale revivescens sessilis vel in substrata decurrens, crebro nodulosa in sulcis trunci leviter evoluta, quandocunque valide evoluta imbricata, tenax coriacea in sicco rigida dura; pileus applantus vel paullo convexus, 1–4 cm. longus, 2.5–6 cm. diametro 0.4–0.8 cm. crassus, sordido-griseus in sicco fumeus vel nigrescens, pubescens, pilis brevibus velutinis, mox glabratus vel fibrilloso-striatus haud incrustatus uni-vel bizonatus, zonis latis; contextum album tenax in sicco durum zonatum crassitudine 1–5 mm.; pori albi in sicco immutati vel isabellini vel hepatici, tubulis 1–3 mm. longis, oribus circularibus mox angularibus ad irregularibus integris, circa 3–4 pro mm., parietibus crassis; sporidia ellipsoidea vel angusto-ellipsoidea levia hyalina, 4–5 μ longa, 2.5–3.5 μ diametro; basidia 4–5 μ diametro; cystidia nulla; contexti hyphae hyalinae flexuosae pauci-ramosae, parietibus inconspicue incrassatis, 3–7 μ diametro, interdum conspicue nodoso-septatae.

Hab. ad basim truncorum *Cupressi macrocarpae* Hartweg.

Sporophore annual or reviving with only marginal growth, sessile or decurrent on substratum, frequently poorly developed and nodulose in furrows on the trunk, imbricate where well developed, tough and leathery when fresh, rigid and hard on drying; pileus applanate or somewhat convex 1–4 × 2.5–6 × 0.4–0.8 cm., dirty grayish, becoming grayish brown or blackish on drying, at first with short velvety pubescence, later nearly glabrous or fibrillose-striate, not incrusted, with one or two broad zones or depressions; context white, tough, drying hard, zonate, 1–5 mm. thick; pore surface white when fresh, unchanged in drying or becoming isabelline or dirty buff, the tubes 1–3 mm. long, their mouths circular then subangular to irregular, thick-walled, entire, averaging 3–4 per mm.; spores ellipsoid or narrow ellipsoid, smooth, hyaline, 4–5 × 2.5–3.5 μ; basidia 4–5 μ diam.; cystidia none; context hyphae hyaline, flexuous, sparingly branched, the walls not conspicuously thickened, 3–7 μ diam., with conspicuous though not abundant clamps.

On the lower portion of the trunks *Cupressus macrocarpa* Hartweg.

Type collected at Berkeley, California, Feb. 14, 1923 by (H. E. Parks Herb. 1431; Overholts Herb. 8527); also collected in the same locality and on the same host by Lee Bonar.

"Mr. Bonar has contributed largely to the description here presented. The species has the aspect of a trametoid and over-developed *Polyporus versicolor,* but the spores are very different. From *Fomes annosus* it differs in the less globose spores, in the clamped context hyphae, and in being associated with a very different rot."

Monterey Cypress (*Cupressus macrocarpa* Hartw.), the host of *P. basilaris,* is a narrow endemic in the vicinity of Monterey, California. It occurs indigenously only on the coastal bluffs seldom more than a half mile inland in the region of Monterey. The tree, in spite of its very restricted natural habitat, is readily propagated and has been extensively planted as an ornamental, particularly in California. Certain facts: viz., that the sporophore is a small inconspicuous annual appearing only during moist weather, that the host is not widely distributed, and that the sporophores are relatively rare, are largely responsible for the obscurity of the fungus. In addition, the sporophore usually arises in the natural crevices and convolutions of the trunk, dries out rapidly, and changes color from a smoky-gray to a brown color which blends with the color of the bark and makes detection difficult. Insects frequently attack the sporophores and reduce them in a few weeks to an unrecognizable form.

The stands of *C. macrocarpa* from which data for this paper were obtained were as follows: (1) in the vicinity of the Greek Theatre on the University of California campus at Berkeley, trees planted in 1867; (2) in Sequoia Park in the Oakland Hills, at an elevation 800 feet higher than stand (1); (3) in Golden Gate Park, San Francisco, California; (4) in the vicinty of Monterey, California.

Because of a blight, caused by *Coryneum* sp., and a bark beetle, *Phloeosinus cupressi* Hopk., which had infected the cypress, many of the trees in these areas were being cut to check further infection. This offered an opportunity to make observations on freshly sectioned trunks. A pocket rot was found to be common in all of the older trees in the above-mentioned

TABLE 1

Number of trees in four stands of C. macrocarpa containing pocket rot associated with Polyporus basilaris.

Location	No. of trees	Trees with rot	Percentage with rot	Average age
U. C. Campus	78	70	88.5	65 years
Sequoia Park	349	5	1.43	26 "
Golden Gate Park	81	15	18.5	34 "
Monterey	83	68	82.0	No estimate

stands. Data were obtained on the diameter of the trunks and the amount of rot shown in cross section at stump height, approximately 2 feet above ground.

More detailed studies were made on trees in the campus stand. These included sketches of cross and longitudinal sections of the base of the trunk and estimates of the area of decay, the longitudinal extent of the rot, and the presence or absence of the rot in the roots. Trunks of two trees were split longitudinally into quarters and the sections sketched and measured in order to compare the actual amount of sound and decayed wood. It was found from this more detailed study of 71 trees that 32 per cent contained only a small amount of decay (¼ to 5 square inches as shown in cross-section). However, all the trees over three feet in diameter showed infection, and 60 per cent of these contained over 50 square inches of decay. All cross-section measurements were made at stump height.

The pocket rot so commonly found in the trunk of the tree is found less commonly in the roots. In the larger roots it may penetrate a few inches but generally not to any great depth. On the campus it was possible to make a study of the root system because the trees were pulled down and their roots thus exposed. While 20 per cent of the trees were found to contain occasional pockets of rot in their roots, badly infected trees seldom showed more than two or three small pockets in the entire root system.

Cross and longitudinal sections of the cypress trunks show that the infection of the tree ordinarily takes place in the lower part of the trunk. In young trees, in which the rot was in the incipient stages, the infection was without exception present in the lower portion of the tree. The height of the rot as determined from an examination of thirty-two trees was as follows: twenty-six of the trees were found to have the rot limited to less than twelve feet above the ground line and only five exceeded this height. The highest extension of the rot found in the trunk of any cypress was seventeen feet. In this tree it was found to be present in the larger branches.

In trees showing the beginning stages of decay a cross-section of the trunk often has but a single pencil of rot. When sections of such trees are split longitudinally, these pencils may be traced for a distance of a few inches to two feet, depending upon the degree of development of the rot. The infected wood in the incipient stage is almost normal in appearance, but usually tinged with yellow. These infected pockets, upon drying out, become darker in color and show fine checks. In badly decayed trees one or more pencils of rot may be found on the advancing line of decay. The decay does not proceed into uninfected areas as an ever increasing spherical mass of rot, but rather spreads by means of long finger-like protrusions into the heartwood. As the rot proceeds, it becomes very complete, leaving a brown crumbly residue which cracks into square or rectanglar blocks. In the advanced stages of decay the pockets coalesce so that they form masses of rot with thin irregular strips of firm wood scattered through the mass. Wefts of white mycelium frequently appear in the cracks of the rot. There is no apparent discoloration in the wood beyond the sharp border of the pockets.

Microscopic examination of the decayed wood showed that the hyphae were rare in the pockets of rot. However, they are found abundantly in a zone about six millimeters wide between the border of the pocket of rot and the sound wood. The hyaline hyphae are 0.7–1.5 μ in diameter and branch freely as they pass from one cell to another. The penetration of the cell walls may be through bordered pits or directly through the wall. Tissue cultures made from the edges of the pockets and from the incipient stages of decay bear out the results obtained from the microscopical studies, i.e., that active mycelium is found only in a narrow margin around the pocket of rot. Negative results in culture tests were obtained from wood beyond 6 mm. from the border of the pockets and from the sound wood between the pockets. Extremely decayed wood either failed to produced any fungus in culture, or, as was generally the case, was contaminated with other fungi, such as various species of *Penicillium* and *Trichoderma.*

Three other basidiomycetes have been reported on *Cupressus macrocarpa:*[1] *Polyporus carbonarius* Murrill, *Polyporus cutifractus* Murrill, and *Hydnum ochraceum* (Pers.) Fries. However, during this investigation no fruiting bodies other than those of *P. basilaris* have been collected from Monterey cypress.

Figure 1 shows isolated pockets as they appear in cross section; figure 2 shows a longitudinal section from the bole of the tree with pockets of rot extending upward from the generally rotted base. This condition of the base probably arose from the single pocket which increased in size and at the same time formed branch pockets.

Every sporophore collected has been found to arise from the main part of the trunk, usually in the vicinity of decayed knots. If the point of origin of the sporophore is any indication of the original point of infection, as it is considered to be in some instances, this would be added proof that infection occurs through the base of the tree.

One or more sporophores may develop on a single cypress tree and as many as four have been collected from a single trunk during the same season. Fruiting bodies have been collected on old stumps as well as on trunks of living trees. Longitudinal sections of the trunk cut at the point of infection often show the rotted wood in the vicinity of the sporophore to be thoroughly moist. The presence of moisture is probably important in the development of the sporophores. In the Berkeley region they appear during the rainy season, usually in the latter part of November or the early part of

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[1] Seymour, A. B., Host index of the fungi of North America, p. 72. 1929.

December. From then on they may continue to develop until the middle of February, or later, although the majority of sporophores have usually passed their prime and many have ceased to sporulate by that time.

The sporophores first appear as nodular fleshy sheets of grayish tissue. From these foundations shelves appear, growing from the upper marginal part of the sporophore. Frequently one finds cavities which are completely shut off from the outside and yet contain well developed spore-producing tubes inside. These cavities are particularly common in the older parts of sporophores where there has been a growing over or coalescing of one shelf of the sporophore with another. Sporophores have been found to recur season after season on the same trees and in the same places on the trunk. Mature sporophores vary greatly in type, size, and shape. The imbricate shelving type is the most commonly found (figure 3), but one finds also sporophores which are resupinate, nodulose, or even fleshy "sparassus" types.

Tissue cultures from the sporophores of *P. basilaris* frequently produce Poria-like fruiting bodies on agar slants and in Petri dishes (figure 4). If the test tube or the Petri dish is inverted so that the spores may collect on the lid, a heavy coating of spores is deposited on the glass. Abortive sporophores may also develop on blocks of wood. The under surface of such sporophores is composed of lamella-like rays. Sporulation has not, however, been observed to occur from these fruiting bodies.

Sporulation in nature may continue over a period of several weeks. Daily observations have showed that some of the fruiting bodies may shed spores continuously for a month and a half. The average period of sporulation, however, is about half of this time. From large sporophores sporulation is often so heavy that during an interval of twenty-four hours a glass slide placed underneath will have a heavy white coating.

Spores of *Polyporus basilaris* have a very low percentage of germination in culture. Samples for the germination studies were obtained from the field on sterile glass slides by the use of spore traps, or, in some cases the whole sporophore was collected and allowed to shed spores directly upon the medium. Spores were gathered from different sporophores. Substrata of various compositions and pH were used, but negative results in the spore germination studies were obtained except with one medium, containing

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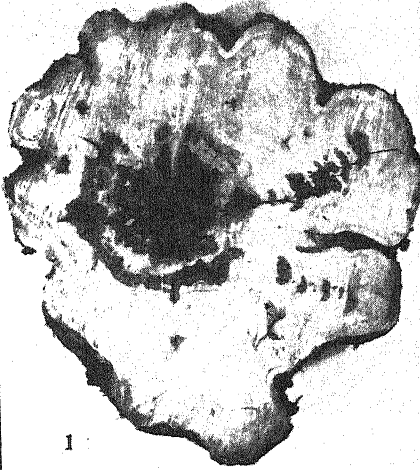
Explanation of figures 1–4.

FIG. 1. Cross-section through trunk of *Cupressus macrocarpa* showing isolated pockets of rot outside the generally rotted center. FIG. 2. Longitudinal section through lower portion of trunk of *Cupressus macrocarpa* showing pockets of rot extending upwards from a generally rotted base. FIG. 3. Sporophore of *Polyporus basilaris*, typical imbricate type. FIG. 4. *a*, Surface view of Petri dish containing a block of wood of *Cupressus macrocarpa* on a glass plate over a young culture of *Polyporus basilaris*; *b*, rotted wood block after exposure to the fungus 120 days; *c*, sporophore of *Polyporus basilaris* developing on wood block in culture.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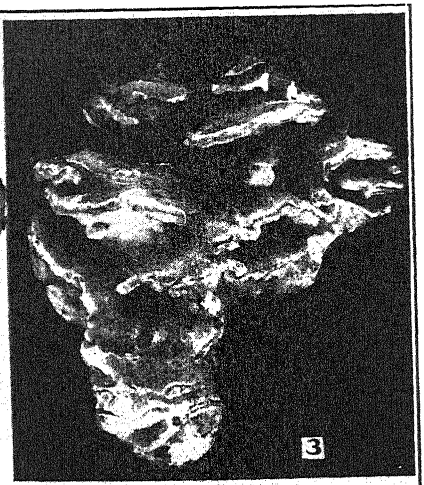
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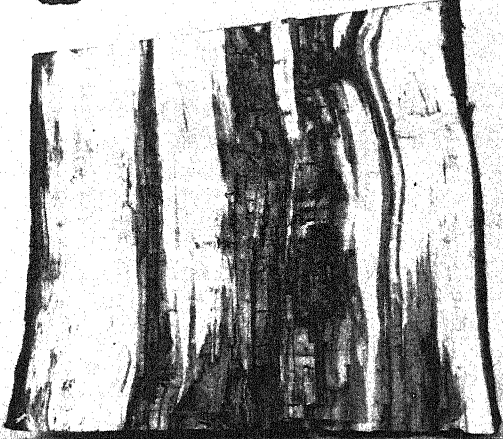
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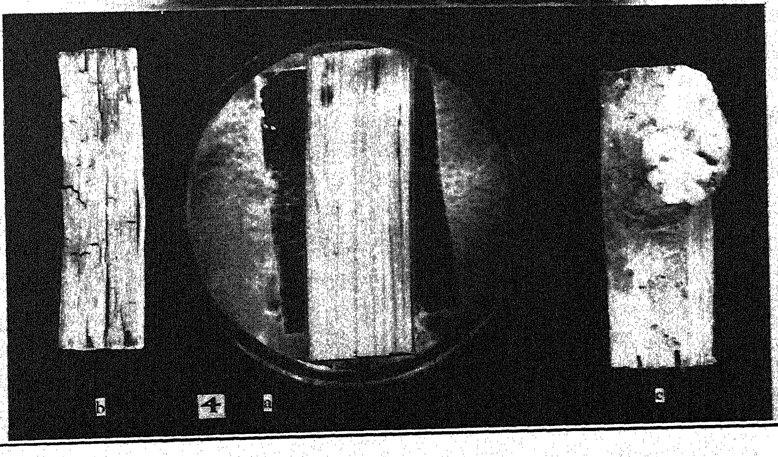
4

1 per cent peptone, 1 per cent glucose, and 2 per cent agar, with a few shavings of *C. macrocarpa*. The spores from a spore suspension were dispersed on the substrate with a sterile platinum loop. An examination of the plates two days after inoculation showed that approximately 50 per cent of the spores had germinated. Later attempts with the same medium did not prove successful.

In order to study the effect of the rot on the wood, artificial inoculation was undertaken in the laboratory. The procedure used in preparing sound wood for inoculation was as follows: A section of trunk 16 inches in diameter was sawed into blocks one inch square by three inches long. These were soaked in water under a bell jar for about an hour at reduced pressure. They were then sterilized in an Arnold sterilizer on three successive days for periods of a half hour. At the conclusion of this treatment a moisture content of 40–50 per cent was obtained, as determined by weighing samples, then drying out these samples and reweighing. The blocks of wood were then removed aseptically from the containers in which they were sterilized and placed on sterile glass slides in specially prepared culture dishes; these contained a growth of mycelium of *P. basilaris*, with which they had been inoculated. The culture dishes had been prepared some days previous to the preparation of the blocks of wood, so that the fungus isolated from the tissue of the sporophore could develop a heavy mat of mycelium. Two per cent malt extract agar was used as a culture medium. The dishes containing the blocks of wood were then placed in a humid chamber at 25° C ± 3°. Starting the wood to rot over a young vigorous mat of mycelium considerably shortens the time required to rot the wood. By this method several points of infection occur at once and the fungus is able to maintain itself on the nutrient until it becomes established on the wood.

The growth of the mycelium of *P. basilaris* over the blocks of *C. macrocarpa* in culture is rather slow. Only a thin threadlike reticulum of interwoven hyphae covers the surface of the block of wood in a sparse white growth. A block of wood split lengthwise with the grain, however, shows that the fungus penetrates the wood readily. A thin white coating of mycelium can sometimes be observed on the freshly split surface. The wood seems waxy to the touch. In the last stages of decay it is brittle, and when it dries out many fine cracks develop (fig. 4*b*).

Chemical analyses were made at three periods during the process of decay so that various changes in the composition of the wood could be noted. Preparation for the analyses was as follows: Wood blocks which had been exposed to the activity of the fungus for a certain period were taken from culture, dried, and the loss in weight determined. The rotted wood was then ground, sieved, and divided into 60–80 mesh and 80–100 mesh samples. The sawdust used in the sound wood analysis was prepared by holding a rasp against a block of wood as it was turned on a lathe. The method of the Forest Products Laboratory[2] was used in the analysis of the wood samples except as follows: the water soluble component was determined by extracting, with the use of a Soxlet extractor, for four hours at a temperature of 85° C. The chlorine gas was only approximately measured and no cooling system was used around the chlorinating chamber. Although these changes in procedure are not conventional, any method of wood analysis now available is subject to criticism. The results showed, in general, that there was a progressive utilization of wood components in the wood. Samples taken at successive intervals during exposure to the fungus showed losses in weight of 10.2, 18.1, and 39 per cent. Table 2 shows the relative percentages of the components of the rotted wood, sound wood, and sporophore tissue. The values obtained from the sporophore tissue differ in several respects from those of the sound and decayed wood.

TABLE 2

Analysis of sound and decayed wood of Cupressus macrocarpa and sporophore tissue of Polyporus basilaris.

	Wood decayed in culture			Sound wood	Sporophore
Loss in weight	10.2%	18.1%	39.0%		
Water soluble	10.68	10.19	11.50	11.05	30.14
Alcohol benzene soluble	6.91	4.18	3.78	9.77	16.0
Cellulose	40.94	32.83	18.48	46.2	43.4
Lignin	17.87	30.8	22.8	31.1	13.35
Pentosans	12.78	10.57	6.53	8.62	26.9
Ash	0.476	0.516	0.27	0.339	....

SUMMARY

(1) A study made in the field on the occurrence of the pocket rot caused by *P. basilaris* in *C. macrocarpa* showed that only 2 per cent of the trees were infected by the time they were 26 years old, while in another stand 88 per cent of the trees were infected at the average age of 65 years.

(2) The rot caused by *P. basilaris* was found to be limited to the bole of the tree. Only occasionally was it present in the branches and roots.

(3) In the incipient stages of decay only small pockets of rot were found. These grew in size and finally coalesced to form large masses of decayed wood.

(4) Sporophores recurring season after season have been found on both living and dead cypress trunks. Sporulation from these was found to occur for periods up to 45 days. Sporulating fruiting bodies were obtained in culture and spore germination secured.

(5) *P. basilaris* was grown in culture on specially prepared wood blocks of *C. macrocarpa* and the rate of growth found to be very slow.

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[2] Bray, M. W., in Paper Trade Jour. 87(25): 59–68. 1928.

(6) Analyses made on wood samples from blocks which had lost 10.2, 18.1, and 39 per cent weight during the process of decay showed a progressive utilization by the fungus of many of the components of the wood.

The author is greatly indebted to Dr. Lee Bonar, Department of Botany, University of California, who began the original investigation on *Polyporus basilaris*. His helpful advice and constant encouragement have been much appreciated.

BERKELEY, CALIFORNIA

NEW COMBINATIONS AND NEW NAMES IN THE UMBELLIFERAE

Mildred E. Mathias and Lincoln Constance

The authors have been preparing a revision of the Umbelliferae for North American Flora. The purpose of this paper is to list certain new combinations and new names.

Arracacia Bancr. in Jamaica Jour. 4: 18. 1826. The following new combinations and new names are necessary:

Arracacia arguta (Rose) Mathias & Constance, comb. nov. *Museniopsis arguta* Rose, Contr. U. S. Nat. Herb. **8**: 336. 1905. *Tauschia drudeophytoides* Macbr., Contr. Gray Herb. n. s. **56**: 33. 1918.

Arracacia atropurpurea (Lehm.) Benth. & Hook. var. **brevipes** (Coult. & Rose) Mathias & Constance, comb. nov. *Arracacia brevipes* Coult. & Rose, Contr. U. S. Nat. Herb. **3**: 296. 1895.

Arracacia anomala Mathias & Constance, nom. nov. *Museniopsis pubescens* Coult. & Rose, Proc. Wash. Acad. **1**: 134. 1900. Not *Arracacia pubescens* Wolff, 1910. *Tauschia pubescens* Macbr. Contr. Gray Herb. n. s. **56**: 33. 1918.

Arracacia tolucensis (HBK) Hemsl. var. **multifida** (Wats.) Mathias & Constance, comb. nov. *Arracacia multifida* Wats. Proc. Amer. Acad. **26**: 136. 1891. *Arracacia dissecta* Coult. & Rose, Proc. Wash. Acad. **1**: 141. 1900. *Arracacia Dugesii* Coult. & Rose, op. cit., p. 141. *Arenaria multifida* Wats. ex Durand & Jackson, Ind. Kew Suppl. **1**: 36. 1902, error. *Arracacia tenuifolia* Rose, Contr. U. S. Nat. Herb. **10**: 127. 1906.

Arracacia Schiedei (Wolff) Mathias & Constance, comb. nov. *Nematosciadium Schiedei* Wolff in Fedde, Repert. **9**: 419. 1911.

Tauschia Schlecht. Linnaea **9**: 607. 1834. Not *Tauschia* Preissler, 1828. *Deweya* Torr. & Gray, Fl. N. Amer. **1**: 641. 1840. *Museniopsis* Coult. & Rose, Rev. N. Amer. Umbel. 26, 122. 1888, as to type species only. *Hesperogenia* Coult & Rose, Contr. U. S. Nat. Herb. **5**: 203. 1899. *Drudeophytum* Coult. & Rose, Contr. U. S. Nat. Herb. **7**: 80. 1900. *Valaea* DC. of authors in part.

Macbride[1] was correct in referring these various species to the one genus *Tauschia* Schlecht. which has been conserved over *Tauschia* Preissler. The following new combinations are necessary:

Tauschia glauca (Coult. & Rose) Mathias & Constance, comb. nov. *Velaea glauca* Coult. & Rose, Contr. U. S. Nat. Herb. **3**: 321, *pl. 14*. 1895. *Drudeophytum glaucum* Coult. & Rose, Contr. U. S. Nat. Herb. **7**: 82. 1900. *Veleae glauca* var. *purpurascens* J. T. Howell, Leafl. West. Bot. **2**: 185. 1939.

Tauschia Stricklandi (Coult. & Rose) Mathias & Constance, comb. nov. *Hesperogenia Stricklandi* Coult. & Rose, Contr. U. S. Nat. Herb. **5**: 203, *pl. 27*. 1899. *Zizia Stricklandi* K.-Pol. Bull. Soc. Nat. Mosc. n. s. **29** (1915): 200. 1916.

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[1] Macbride, Contr. Grey Herb. n. s. **56**: 28. 1918.

Tauschia tenuifolia (Wats.) Mathias & Constance, comb. nov. *Eulophus tenuifolius* Wats. Proc. Amer. Acad. **23**: 276. 1888. *Velaea tenuifolia* Drude in Engl. & Prantl, Pflanzenfam. **3** (8): 169. 1898. *Museniopsis tenuifolia* Coult. & Rose, Contr. U. S. Nat. Herb. **3**: 302. 1895.

DONNELLSMITHIA Coult. & Rose, Bot. Gaz. **15**: 15. 1890. *Museniopsis* Coult. & Rose, Rev. N. Amer. Umbel. 26, 122. 1888, as to Mexican species, not as to type species. *Schiedeophytum* Wolff, in Fedde Repert. **9**: 419. 1911.

The genus *Donnellsmithia*, based on the species *D. guatemalensis*, has been considered monotypic. This study has shown that the numerous Mexican species referred to *Museniopsis* and the monotypic genera *Donnellsmithia* and *Schiedeophytum* constitute a natural generic unit for which the name *Donnellsmithia* must be used. The following new combinations are necessary.

Donnellsmithia biennis (Coult. & Rose) Mathias & Constance, comb. nov. *Museniopsis aegopodioides* Coult. & Rose, Contr. U. S. Nat. Herb. **3**: 302. 1895, as to specimens cited, not as to synonymy and not including name-bearing synonym. *Museniopsis biennis* Coult. & Rose, Proc. Wash. Acad. **1**: 130. 1900. *Tauschia biennis* Macbr. Contr. Gray Herb. n. s. **56**: 32. 1918.

Donnellsmithia cordata (Coult. & Rose) Mathias & Constance, comb. nov. *Museniopsis cordata* Coult. & Rose, Contr. U. S. Nat. Herb. **3**: 304. 1895. *Museniopsis scabrella* Coult. & Rose, op. cit., p. 304. *Velaea cordata* Drude in Engl. & Prantl, Pflanzenfam. **3** (8): 169. 1898. *Velaea scabrella* Drude, op. cit., p. 169. *Tauschia scabrella* Macbr. Contr. Gray Herb. n. s. **56**: 33. 1918.

Donnellsmithia dissecta (Coult. & Rose) Mathias & Constance, comb. nov. *Museniopsis dissecta* Coult. & Rose, Contr. U. S. Nat. Herb. **3**: 304. 1895. *Velaea dissecta* Drude in Engl. & Prantl, Pflanzenfam. **3** (8): 169. 1898. *Tauschia pinetorum* Brandegee, Univ. Calif. Publ. Bot. **10**: 413. 1924.

Donnellsmithia madrensis (Coult. & Rose) Mathias & Constance, comb. nov. *Museniopsis madrensis* Coult. & Rose, Proc. Wash. Acad. **1**: 130. 1900.

Donnellsmithia mexicana (Robins.) Mathias & Constance, comb. nov. *Pimpinella mexicana* Robins. Proc. Amer. Acad. **26**: 164. 1891. *Schiedeophytum fallax* Wolff in Fedde, Repert. **9**: 420. 1911. *Schiedeophytum mexicanum* Wolff in Engl. & Prantl, Pflanzenr. **90**: 326. 1927.

Donnellsmithia ovata (Coult. & Rose) Mathias & Constance, comb. nov. *Museniopsis ovata* Coult. & Rose, Proc. Wash. Acad. **1**: 133. 1900. *? Museniopsis biennis* var. *pinnatisecta* Riley, Kew Bull. **1924**: 22. 1924.

Donnellsmithia peucedanoides (HBK) Mathias & Constance, comb. nov. *Cnidium peucedanoides* HBK. Nov. Gen. et Sp. **5**: 15. 1821. *Eulophus peucedanoides* Benth. & Hook. Gen. Pl. **1**: 885. 1867. *Eulophus ternatus* Wats. Proc. Amer. Acad. **23**: 276. 1888. *Museniopsis peucedanoides* Coult. & Rose, Contr. U. S. Nat. Herb. **3**: 303. 1895. *Museniopsis ternata* Coult. & Rose, op. cit., p. 303. *Museniopsis ternata* var. *filifolia* Coult. & Rose, op. cit. p. 303. *Museniopsis Schaffneri* Coult. & Rose, op. cit., p. 303. *Velaea peucedanoides* Drude in Engl. & Prantl, Pflanzenfam. **3** (8): 169. 1898. *Velaea ternata* Drude, op. cit., p. 169. *Velaea Schaffneri* Drude, op. cit., p. 169. *Tauschia peucedanoides* Macbr. Contr. Gray Herb. n. s. **56**: 32. 1918. *? Peucedanum junceum* Humb. & Bonpl. ex Spreng. in Roem. & Schult. Syst. Veg. **6**: 572. 1820.

DONNELLSMITHIA PEUCEDANOIDES (HBK) Mathias & Constance var. **purpurea** (Coult. & Rose) Mathias & Constance, comb. nov. *Museniopsis purpurea* Coult. & Rose, Proc. Wash. Acad. **1**: 132. 1900.

Donnellsmithia reticulata (Coult. & Rose) Mathias & Constance, comb. nov. *Museniopsis reticulata* Coult. & Rose, Proc. Wash. Acad. **1**: 133. 1900.

Donnellsmithia serrata (Coult. & Rose) Mathias & Constance, comb. nov. *Museniopsis serrata* Coult. & Rose, Contr. U. S. Nat. Herb. **3**: 304. 1895. *Velaea serrata* Drude in Engl. & Prantl, Pflanzenfam. **3** (8): 170. 1898.

Donnellsmithia submontana (Coult. & Rose) Mathias & Constance, comb. nov. *Museniopsis submontana* Coult. & Rose, Proc. Wash. Acad. **1**: 131. 1900.

Donnellsmithia tuberosa (Coult. & Rose) Mathias & Constance, comb. nov. *Museniopsis tuberosa* Coult. & Rose, Contr. U. S. Nat. Herb. **3**: 303. 1895. *Velaea tuberosa* Drude in Engl. & Prantl, Pflanzenfam. **3** (8): 169. 1898. *Museniopsis tenuissima* Coult. & Rose, Proc. Wash. Acad. **1**: 131. 1900. *Museniopsis glauca* Coult. & Rose, op. cit., p. 131. *Museniopsis fusiformis* Rose, Contr. U. S. Nat. Herb. **8**: 337. 1905. *Tauschia fusiformis* Macbr. Contr. Gray Herb. n. s. **56**: 32. 1918.

LEPTOTAENIA Nutt.

Leptotaenia Hendersoni (Coult. & Rose) Mathias & Constance, comb. nov. *Peucedanum Hendersoni* Coult. & Rose, Bot. Gaz. **13**: 210. 1888; Rev. N. Amer. Umbel. 56. 1888. *Leptotaenia Leibergi* Coult. & Rose, Contr. U. S. Nat. Herb. **7**: 202, *pl. 7*. 1900. *Lomatium Hendersoni* Coult. & Rose, Contr. U. S. Nat. Herb. **7**: 209. 1900. *Cogswellia Hendersoni* Jones, Contr. Western Bot. **12**: 33. 1908.

Since the publication of the revision of the genus *Lomatium*[1] the authors have seen specimens of the type collection of *Peucedanum Hendersoni* deposited in the herbarium of the University of Oregon. This species is without question identical with *Leptotaenia Leibergi*.

LIGUSTICELLA Coult. & Rose

Ligusticella Macounii (Coult. & Rose) Mathias & Constance, comb. nov. *Ligusticum Macounii* Coult. & Rose, Contr. U. S. Nat. Herb. **1**: 289. *pl. 23*. 1893. *Orumbella Macounii* Coult. & Rose, Contr. U. S. Nat. Herb. **12**: 446. 1909.

LIGUSTICUM L.

LIGUSTICUM FILICINUM Wats. var. **tenuifolium** (Wats.) Mathias & Constance, comb. nov. *Ligusticum tenuifolium* Wats. Proc. Amer. Acad. **14**: 293. 1879. *Ligusticum oreganum* Coult. & Rose, Contr. U. S. Nat. Herb. **7**: 138. 1900.

LIGUSTICUM PORTERI Coult. & Rose var. **brevilobum** (Rydb.) Mathias & Constance, comb. nov. *Ligusticum brevilobum* Rydb. Fl. Rocky Mts. 613, 1064. 1917.

POLYTAENIA DC.

Polytaenia texana (Coult. & Rose) Mathias & Constance, comb. nov. *Polytaenia Nuttallii* var. *texana* Coult. & Rose, Contr. U. S. Nat. Herb. **7**:

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[1] Mathias, Ann. Mo. Bot. Gard. **25**: 225–297. 1938.

192. 1900. *Pleiotaenia Nuttallii* var. *texana* Coult. & Rose, op. cit. **12**: 448. 1909. *Phanerotaenia texana* St. John, Rhodora **21**: 182. 1919.

RHODOSCIADIUM Coult. & Rose.

The genus *Deanea* Coulter and Rose is referred to *Rhodosciadium*, making the following new combinations and new names necessary:

Rhodosciadium argutum (Rose) Mathias & Constance, comb. nov. *Deanea arguta* Rose, Contr. U. S. Nat. Herb. **10**: 128. 1906.

Rhodosciadium diffusum (Coult. & Rose) Mathias & Constance, comb. nov. *Deanea diffusa* Coult. & Rose, Proc. Wash. Acad. **1**: 155. 1900.

Rhodosciadium longipes (Rose) Mathias & Constance, comb. nov. *Deanea longipes* Rose, Contr. U. S. Nat. Herb. **10**: 128. 1906.

Rhodosciadium macrophyllum Mathias & Constance, nom. nov. *Deanea glauca* Coult. & Rose, Proc. Wash. Acad. **1**: 156. 1900. Not *Rhodosciadium glaucum* Coult. & Rose. 1895.

Rhodosciadium montanum (Coult. & Rose) Mathias & Constance, comb. nov. *Deanea montana* Coult. & Rose, Proc. Wash. Acad. **1**: 155. 1900.

Rhodosciadium Nelsoni (Coult. & Rose) Mathias & Constance, comb. nov. *Deanea Nelsoni* Coult. & Rose, Proc. Wash. Acad. **1**: 155. 1900.

Rhodosciadium purpureum (Rose) Mathias & Constance, comb. nov. *Deanea Pringlei* Rose, Contr. U. S. Nat. Herb. **10**: 128. 1906. Not *Rhodosciadium* Pringlei Wats., 1890. *Deanea purpurea* Rose, op. cit., p. 128.

SPERMOLEPIS Raf.

Spermolepis inermis (Nutt.) Mathias & Constance, comb. nov. *Leptocaulis inermis* Nutt. ex DC. Coll. Mem. **5**: 39, *pl. 10, f. b.* 1829. *Leptocaulis patens* Nutt. ex DC. Prodr. **4**: 107. 1830. *Apium patens* Wats. Bibl. Ind. **1**: 413. 1878. *Apiastrum patens* Coult. & Rose, Rev. N. Amer. Umbel. 110. 1888. *Spermolepis patens* Robins. Rhodora **10**: 34. 1908. *Spermolepis patens* var. *inermis* Mathias, Brittonia **2**: 243. 1936.

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UNIVERSITY OF CALIFORNIA
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INDEX TO AMERICAN BOTANICAL LITERATURE

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

Papers that relate exclusively to bacteriology, forestry, agriculture, horticulture, manufactured products of vegetable origin, or laboratory methods are not included. If users of the Index will call the attention of the editor to errors or omissions, their kindness will be appreciated.

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FURTHER POLLEN STUDIES OF POST PLEISTOCENE BOGS IN THE PUGET LOWLAND OF WASHINGTON[1]

HENRY P. HANSEN

(WITH TWO FIGURES)

INTRODUCTION

The modification of the topography by Pleistocene glaciation and the humid climate in the Puget Sound basin of western Washington has been favorable for the development of a larger number of bogs than in other areas of the Pacific northwest. The peat deposits are representatively located, and because the entire region is more or less homogeneous in topography, soil, climate, and phytogeography, pollen analyses of well-distributed bogs should reconstruct a fairly accurate picture of postglacial forest succession and general climatic trends. This study is concerned with further pollen analyses of peat deposits located within this physiographic province. Four other deposits, two in southwestern British Columbia and two near Seattle, have been previously studied, and all six pollen profiles seem to agree essentially on the indicated postglacial forest succession (Hansen 1938, 1940a). This region was glaciated by both the Admiralty and the Vashon glaciers of the Pleistocene (Bretz 1913), and the latter has been generally correlated chronologically with the Wisconsin glaciation of the middle west (Antevs 1929). Fenneman (1931) classifies this region as the Puget Trough of the Pacific Border Province.

The first bog is located a few miles north of Black Diamond, King County, in sect. 35 of T. 22 N., R. 6 E., approximately 20 miles east of Puget Sound, and at an elevation of about 450 feet above sea level. The depression in which it has been developed apparently was formed in irregular ground moraine or by damming of a small preglacial stream valley. The surrounding terrain is irregular and covered with glacial drift but is not extremely rugged. The bog is surrounded by a marginal ditch that supports a dense growth of willow (*Salix Scouleriana*) and hardhack (*Spiraea Douglasii*). Near the northern margin a shallow, intermittent pond persists wherein grow yellow pondlily (*Nymphozanthus polysepala*), buckbean (*Menyanthes trifoliata*),

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and *Dulichium arundinaceum*. The central and larger area is covered chiefly with Labrador tea (*Ledum groenlandicum*), bog laurel (*Kalmia polifolia*), cotton grass (*Eriophorum gracile*), buckbean, sedge (*Carex* spp.), *Sphagnum* sp., and *Polytrichum juniperinum*. An extensive zone of hardhack surrounds this community and is gradually encroaching upon it. An invasion by lodgepole pine (*Pinus contorta*) was under way, but has been destroyed by fire. On higher ground adjacent to the bog grow red alder (*Alnus rubra*), largeleaf maple (*Acer macrophyllum*), vine maple (*A. circinatum*), ocean spray (*Holodiscus discolor*), syringa (*Philadelphus Gordonianus*), Oregon ash (*Fraxinus oregana*), elderberry (*Sambucus callicarpa*), blueberry (*Vaccinium ovatum*), salal (*Gaultheria shallon*), dewberry (*Rubus macropetalus*), fireweed (*Epilobium angustifolium*), bracken fern (*Pteridium aquilinum*), and Douglas fir (*Pseudotsuga taxifolia*). Many other herbaceous plants also exist in this community.

Peat samples were obtained with a Hiller borer at quarter-meter intervals. The depth of the bog approximately in the center is 6 meters and it is underlain with sand. There are greater depths indicated by a profile taken by Rigg and Richardson (1938). The lower quarter meter consists of silt, followed by limnic peat grading at 4 meters into fibrous peat which is present to the surface. Volcanic ash crystals occur at the 2-meter level, while in other parts of the bog ash exists as a well-defined layer. Ash is present in most of the bogs in the Pacific northwest, and may occur as a layer or dispersed crystals, which is apparently determined by the stage of hydrarch succession at the time of eruption. *Sphagnum* leaves first appear at 3.5 meters.

The other bog is located about 3 miles north of Sedro Woolley, Skagit County, in sect. 31 of T. 36 N., R. 5 E. It lies about 12 miles east of Puget Sound and almost 100 miles north of the former bog. The depression in which it has been formed had its origin as a kettle pond in terraced outwash of the Samish River. The elevation is about 350 feet above sea level, and the foothills of the Cascade Range rise immediately to the east. The bog comprises about 80 acres, with a deep lake persisting in the center. A submerged hydrosere exists in the lake, with a floating hydrosere of pondweed (*Potamogeton natans*) and yellow pondlily near the shore. Along the shore grow clumps of cattail (*Typha latifolia*), purple marshlocks (*Potentilla palustris*), sedge, and *Sphagnum*. Farther inland thrive Labrador tea, bog laurel, cranberry (*Vaccinium oxycoccus*), and hardhack. On the margin of the bog are alder, willow, and other shrubby plants similar to those around the other. The southern portion is annually mowed for hay, while on the northern margin it is being sparingly invaded by trees, including western hemlock (*Tsuga heterophylla*), western white pine (*Pinus monticola*), and lodgepole pine. Peat samples were obtained with a Hiller borer at quarter-meter intervals about 50 feet south of the lake. Here the lacustrine deposits are 9.5 meters deep, the lower two and one-quarter meters composed of blue clay with a distinct metallic sheen. This was probably carried into the lake in late glacial or early postglacial time before the invasion of forests, as it is entirely devoid of pollen. The clay changes into dark limnic peat at 7.25 meters, which in turn grades into brown fibrous peat at 4 meters; the latter is present to the surface. *Sphagnum* leaves first appear at 6.5 meters. No volcanic ash was found, either as a layer or dispersed crystals.

FORESTS IN ADJACENT AREAS

Since both bogs lie within the same physiographic, climatic, and phytogeographic province, a discussion of the general phytosociological aspects may be applied to areas in the vicinity of both. All of the Puget lowland in western Washington lies within the Humid Transition life zone (Piper 1906). The most characteristic tree of this zone is Douglas fir, and before lumbering, fire, and cultivation removed the virgin forest it was the predominant tree in most areas. Clements' classification of the major vegetation climaxes of North America includes the Puget Sound lowland in the hemlock-cedar association of the Coast Forest (Weaver and Clements 1938). In this formation western hemlock, western red cedar (*Thuja plicata*) and Douglas fir are the chief dominants, the latter persisting as a subclimax species because of its aggressiveness in invading areas denuded by fire. However, the seedlings of Douglas fir do not grow on the forest floor, while the more tolerant hemlock, cedar, and lowland white fir (*Abies grandis*) readily gain a foothold and form an understory. The stand of Douglas fir gradually thins out because of wind, insects, disease, and lack of reproduction, whereas the others continue to expand. Eventually, if fire and lumbering do not disrupt normal forest succession, hemlock, cedar, and lowland white fir will form the climax forest with large and mature Douglas fir scattered throughout. Munger (1940), studying the composition of forests of various ages, has shown that without fire or logging a Douglas fir forest would probably be converted to the climax type in five or six centuries. Other conifers of lesser importance in the Humid Transition zone include western white pine, lodgepole pine, Sitka spruce (*Picea sitchensis*), and silver fir (*Abies amabilis*). Western white pine occurs occasionally on open knolls and well drained areas where the climax forest has been removed, and lodgepole pine is often the pioneer invader of bogs or areas where the soil has been disturbed. Sitka spruce is not common but may be locally abundant on swampy floodplains near sea level, while silver fir grows mixed with other conifers at higher elevations. Broadleaf trees and shrubs consist chiefly of red alder, broadleaf maple, Oregon ash, cottonwood (*Populus trichocarpa*), several species of willow, and many other species of shrubs. These plants occur abundantly on favorable sites as members of associes, facies, and socies. The western boundary of the Canadian zone occupying higher altitudes lies about 20 miles to the east of both bogs.

Forest type maps (1936) indicate 12 forest types within a distance of 8 miles from each bog. Douglas fir types of several size-classes constitute about 75 per cent of the forest cover in the vicinity of the Black Diamond bog. Other types in order of the size of their area are agricultural and non-agricultural lands, recent and non-restocked cutovers, hardwoods, and spruce-hemlock-cedar. Adjacent to the Sedro Woolley bog recent and non-restocked cutovers comprise about 25 per cent of the area, and Douglas fir types of all size-classes comprise an equal area. Other types in order of their area include non-agricultural lands, spruce-hemlock-cedar, hardwoods, and a small area of balsam fir–mountain hemlock–upper slope type. The latter type does not exist within 8 miles of the Black Diamond bog. The spruce-hemlock-cedar type is more extensive and nearer to the Sedro Woolley bog, and is better represented by higher proportions of western hemlock and Sitka spruce pollen in the upper levels. On the other hand, Douglas fir is recorded in a much greater proportion in the upper levels of the Black Diamond bog, because of the large area occupied by Douglas fir types in this vicinity. It is probable that pollen from forests well beyond an 8 mile radius is recorded, but the relative area covered by different forest types adjacent to peat deposits seem to be somewhat proportionately reflected in the upper strata (Hansen 1940b).

In his classification of the climatic provinces of North America, Thornthwaite (1931) designates most of the Puget Sound basin as having a humid, microthermal climate with adequate precipitation at all seasons. Thornthwaite's climatic provinces are based upon the relation between humidity, temperature, and seasonal distribution of precipitation. A small area adjoining the southeastern tip of Puget Sound is indicated as having a similar climate, but with a summer deficiency in precipitation. This area is spoken of locally as the "Tacoma prairies" (Jones 1936), because of the general absence of forests, although at present it is being invaded by oak (*Quercus Garryana*) and Douglas fir. It is possible, however, that the porosity of the gravelly glacial outwash that covers this area and its rapid drainage are more responsible for the dearth of trees than the limited summer rainfall. The mean annual precipitation at Tacoma, Washington, is greater than in other Puget Sound areas that support the hemlock-cedar climax forest. Piper (1906) designated this area as the Humid Transition (prairies) life zone. The mean annual precipitation at Kent, about 10 miles west of the Black Diamond bog is approximately 37 inches, and at Sedro Woolley 47 inches (U. S. Weather Bureau 1936). A higher proportion of the annual precipitation occurs during the growing months at the latter station. The rainfall at Kent, however, is somewhat lower than at higher elevations to the

TABLE 1

Percentages of fossil pollen, Black Diamond Bog.

th in meters:	6.0	5.75	5.5	5.25	5.0	4.75	4.5	4.25	4.0	3.75	3.5	3.25	3.0	2.75	2.5	2.25	2.0	1.75	1.5	1.25	1.0	0.75	0.50	0.25	0.0
is contorta	74	70	76	70	70	26	24	30	20	16	15	10	12	8	16	2	3		4	1	2	1	4	10	4
nonticola	18	21	13	15	12	4	2	6	4	5	6	7	8	14	8	8	6	8	8	4	4	1	1	5	2
idotsuga taxifolia	1	1	1	5	10	50	58	52	61	63	62	62	60	54	52	62	60	45	50	43	47	46	37	36	33
ga heterophylla	1	2	2	2	4	10	4	4	8	8	8	12	11	16	17	20	22	40	33	47	40	45	45	42	54
a sitchensis	5	4	6	4	1	2	4	4	3	4	5	4	4	4	1	2	1	1	1	2	1	3	2	4	1
s grandis	1	2	2	4	3	8	8	4	4	4	4	5	5	4	6	6	8	6	4	3	6	4	11	3	6
is spp.[1]	10	16	19	22	17	11	9	13	7	3	5	7	7	11	12	6	3	2	5	1	3	3			1
nineae[2]			1		1			2	1	1		1	4		2	1	1		1						
positae[2]		2			2						1						1							1	
iopod-Amaranth[2]	1								1													2			
is[2]	18	21	14	19	17	15	13	26	25	22	97	37	110	29	72	35	78	25	30	53	44	31	57	37	64
[2]	1	3	2	6	5	1	1		7	2	14		2	6			3	1	6	2	1	7	1	3	8
la[2]											3	1	2	1	1		10	12	6	5	4	4		2	
x[2]	1			3	1		1			3	1	67	36	33	27	12	3		7	1	2	1		2	7
aceae[2]							1							1			5	1	1		1	2	9	62	8
eraceae[2]	3	2	1	7	1	1	2	7	3	7	5	12	6		3	13	19	10	6	20	17	3	2	3	6
phozanthus[2]					3		2	4	3	3	1	1	3		9	2	4	3	3			4	15		
ia[2]								2	1	1			1			1									

[1] Number of pine pollen grains discarded as unknown, not computed in the percentages.
[2] Number of grains not computed in the percentages.

east in the vicinity of the Black Diamond bog. Greater rainfall occurs at Sedro Woolley because of its location opposite the Straits of Juan de Fuca, while areas farther south in the Puget lowland are protected by the Olympic Mountains.

METHODS

In preparation for study about 2 cc. of peat were boiled in a weak solution of potassium hydrate, strained through cheesecloth, washed, centrifuged, stained with gentian violet, and mounted in glycerin jelly. Exactly 150 significant pollen grains were identified from each level. The non-significant pollen was also recorded but not used in the computation of percentages (tables 1, 2). Non-significant pollen is that from plants growing locally on or near the bog, and is probably not indicative of adjacent forest succession. The significant species recorded as less than 1.5 per cent at any level are listed in the tables as 1 per cent.

The identification of the species of *Pinus* and *Abies* pollen was based on their size ranges as described in a previous paper (Hansen 1940b). For previous papers, as for this, 200 pollen grains of each Pacific northwest species of *Abies, Pinus,* and *Picea* were measured and their size ranges determined. The modern pollen was fossilized with a weak solution of potassium hydrate and mounted in glycerin jelly to simulate the conditions employed in preparing peat slides. All modern pollen was taken from living trees when mature and being shed, rather than from herbarium specimens. In using pollen from dried herbarium specimens there may be danger that the pollen was not fully mature, and had not attained its full size when collected. On the other hand, if the pollen were mature, there is the possibility that most of the pollen had been shed and that the remainder is not normal in size or shape. The latter situation is more significant when the size-variation frequency curve is used in the form of histograms for comparison with the size-variation frequency of fossil pollen. A dearth of pollen of average size was noted by the author for *Pinus contorta, P. ponderosa,* and *P. albicaulis* taken from dried specimens and immature fresh specimens, which will be discussed in a later paper on size-variation frequency of Pacific northwest conifer pollens.

In order of their size beginning with the smallest are *Pinus contorta, P. monticola, P. albicaulis,* and *P. ponderosa;* the firs are *Abies lasiocarpa, A. grandis, A. amabilis,* and *A. nobilis;* and the spruces are *Picea sitchensis* and *P. Engelmanni.* The size range of each species overlaps that of both smaller and larger species, with the exception of lodgepole pine which seems to overlap western white pine slightly or not at all. *Pinus albicaulis* overlaps white and yellow pine, which makes it impractical to attempt to separate this species from the other two. White-bark pine, however, is a timberline tree

TABLE 2

Percentages of fossil pollen, Sedro Woolley Bog.

in meters:	7.25	7.0	6.75	6.5	6.25	6.0	5.75	5.5	5.25	5.0	4.75	4.5	4.25	4.0	3.75	3.5	3.25	3.0	2.75	2.5	2.25	2.0	1.75	1.5	1.25	1.0	0.75	0.5	0.25	0.0
contorta	66	48	32	33	14	24	8	10	7	8	2	5	8	6	1	5	3	6		3		1	2	2	1	2	1	1	1	3
ticola	16	12	7	5	6	2	5	1	2	3	2	1	3	2	2	3	8	2	2	3	3	4	3	2	1	5	8	6	4	10
tsuga taxifolia	5	14	36	46	62	61	60	66	66	61	64	60	48	53	49	40	45	44	35	30	31	30	18	22	28	23	25	26	31	10
heterophylla	1	8	6	8	10	8	15	12	8	12	18	19	27	23	30	33	27	34	47	55	56	53	57	60	50	50	50	51	48	61
sitchensis	10	4	3	3	4	1	2	1	1	1	4	3	4	2	4	2	2	2	6	3	6	6	17	8	16	12	14	14	13	7
grandis	2	13	16	5	4	4	10	10	16	15	10	12	10	14	14	17	15	12	10	6	4	6	3	6	4	8	2	2	3	8
spp.[1]	16	6	3	8	2	5	2	1	1	3		2	4	4		1	7	4	1		3	1	4	1		7	9	6	3	8
neae[2]									1				2	1	1						5		1			1		1	3	5
sitae[2]				1														1											2	3
	23	41	20	46	16	21	15	31	10	55	15	22	6	15	33	37	26	47	20	60	27	33	52	11	30	17	41	57	12	78
	1	3	1	2		1	1	1		1	2		3	1	7	2			7	1		2	6				3			2
[2]								1					1		1		1		1		1	1						2	1	1
	3	1	2			5					7		5	10	2	3	6	3	11	8	9	17	12	1			8	11	2	3
us[2]											1																			
eae[2]		1							1					1	1								1			1		4	1	2
ceae[2]	2	6	3	2	3	1		6	2	6	2	5	3	8	1		2	4	7	11	6	5	6	23	31		7	8	26	11
ozanthus[2]	1	8	6	12	14	6	3	10	2	5	7	8	1	1	1	1			3	6	5	3	6	5	5	1	7	10	6	2
[2]	1	1	6	3	3		1	4	5	5	1	3	5	1	2		12	2	5	3	4		2	2	3		4	2		1

Number of pine pollen grains discarded as unknown, not computed in the percentages.

Number of grains not computed in the percentages.

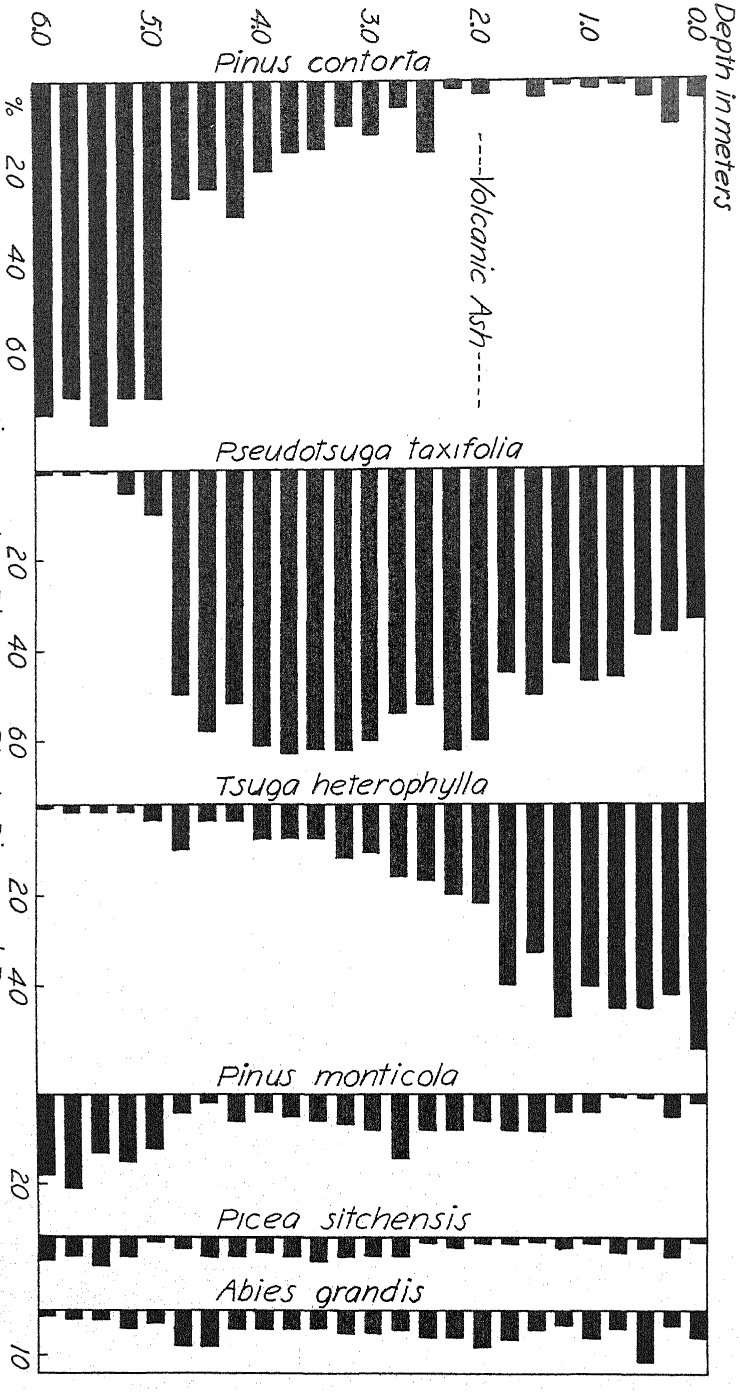

Fig. 1. Pollen Diagram, Black Diamond Bog

and probably never was abundant during postglacial forest succession. Likewise *Abies amabilis* overlaps the smaller *A. grandis* and larger *A. nobilis* and is virtually impossible to separate from these two species. No attempt has been made in this paper to separate silver fir, although all of the fir pollen falls within the range of lowland white fir. Whereas the pollen size ranges of Sitka and Engelmann spruce overlap to some extent, their geographic ranges are not known to overlap in Washington. In this paper it is assumed that all spruce pollen is that of Sitka spruce, because of the low altitude of the bogs and adjacent areas. It is realized, however, that Engelmann spruce pollen may have reached the bogs from higher altitudes to the east. An interesting and important fact was learned recently concerning the pollen of mountain hemlock (*Tsuga Mertensiana*). Pollen of this species collected on Mt. Rainier was found to have bladders, somewhat similar to that of pine, fir, and spruce. It may be differentiated from these species, however, because of the spheroidal cell and fine reticulum of the bladders. Through correspondence with Wodehouse after his examination of the pollen it was found that he had learned of the bladders on mountain hemlock after he had published his book on pollen (1935). He refers to the presence of bladders on fossil hemlock pollen from the Eocene and Tertiary, some with and some without, and all gradations between. Pollen collected from presumably *Tsuga Mertensiana* on the University of Washington campus at Seattle has no bladders, which may indicate a similar gradation for this species. A further check, however, as well as collection of pollen from other trees must be made to verify or refute this possibility. The pollen of *Thuja plicata* seems to be indistinguishable from that of species of *Chamaecyparis*, *Juniperus*, and *Taxus*. Pollen of western red cedar and other similar genera is not well preserved in peat deposits, although cedar is one of the chief dominants in the coast forest. This is evidenced by the apparent absence of cedar pollen in the upper strata of peat deposits even though this tree may live on the bog itself. Observations suggest that western red cedar does not produce as much pollen as pine, Douglas fir, and hemlock, which adds to its degree of under-representation. Pollen profiles are therefore somewhat distorted, especially in the upper levels, since red cedar probably has played no small part in later postglacial forest succession.

In identifying fossil pollen the size of the cell is noted and if within the limits of overlap of other species of the same genus, distorted in shape, broken, or impossible to measure because of its position, it is discarded as an unknown. In previous papers the proportion of conifer pollen thus discarded varied from less than 1 to 12 per cent of the rest of the significant pollen. In this paper the number of discarded pine pollen grains for each level is listed in the tables. The separation of species of pine pollen is not so difficult nor so important in the Puget lowland as in montane bogs east of

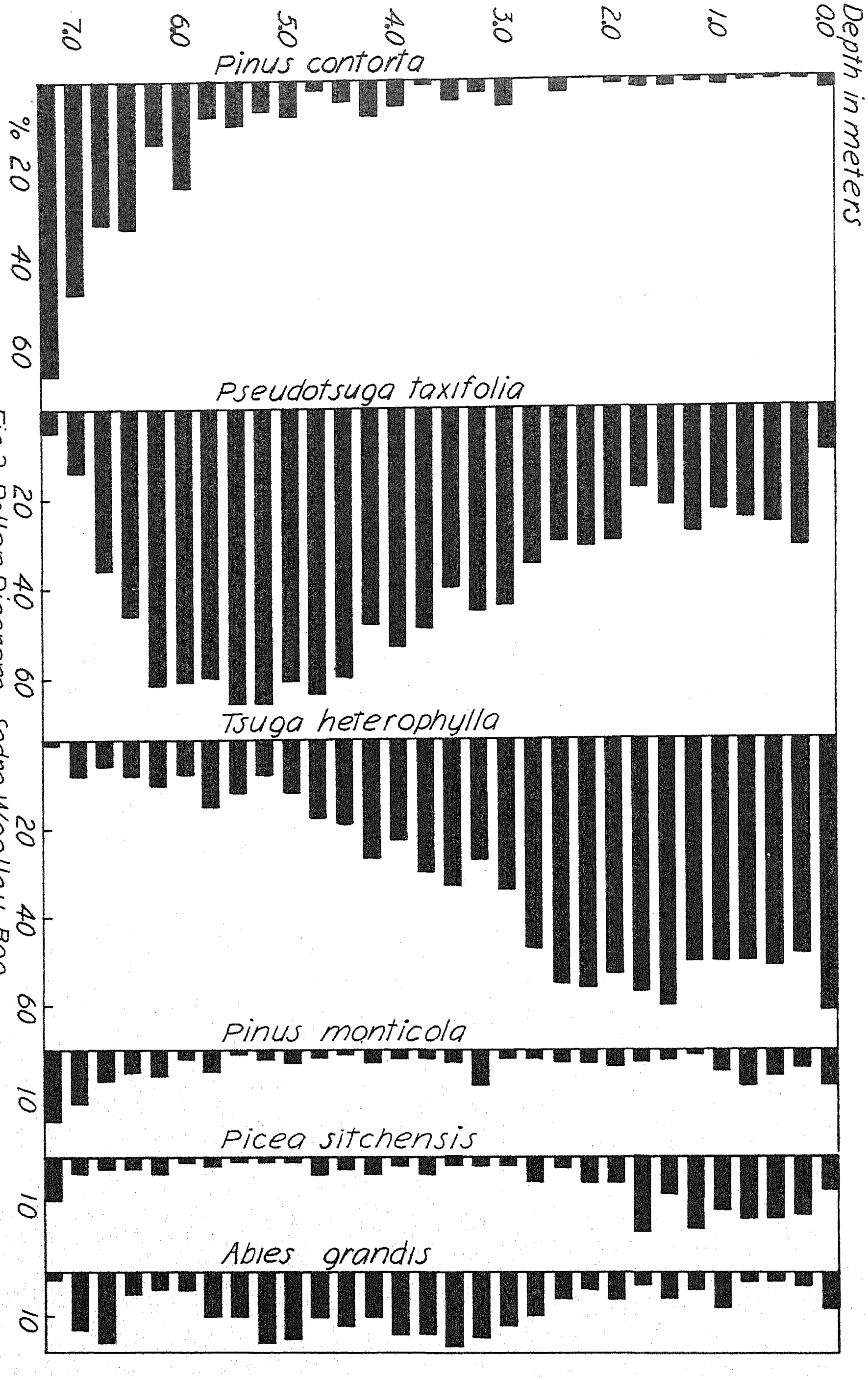

Fig. 2. Pollen Diagram, Sedro Woolley Bog.

the Cascade divide. In the latter region more species are involved and it is much more abundant, since there pine played a far more important role in postglacial forest succession (Hansen 1939a, 1939b, 1939c, 1940b). In the Puget lowland lodgepole and western white pine apparently were pioneer postglacial invaders, and were soon replaced with Douglas fir and western hemlock early in post-Vashon time (Hansen 1938, 1940a).

POSTGLACIAL FOREST SUCCESSION

The pioneer postglacial forests to invade areas adjacent to both bogs consisted largely of lodgepole and western white pine. In the bottom level of the Black Diamond bog the former is recorded as 74 per cent, and in the Sedro Woolley bog as 66 per cent (figs. 1, 2). Western white pine is 18 and 16 per cent respectively in the lowest strata. This record of preponderance of lodgepole pine in early postglacial time corroborates similar evidence indicated by pollen analyses of other bogs in the Puget lowland (Hansen 1938, 1940a). In fact lodgepole pine seems to have been the chief pioneer postglacial invader in most forested regions of the Pacific northwest, regardless of the present climax forest (Hansen 1939a, 1939b, 1940b). In other bogs that may not record all of postglacial forest succession, or are located in glaciated valleys with unglaciated ridges nearby, lodgepole pine is not predominant in the lower levels (Hansen 1939c, 1940c). This suggests that forest succession had already progressed beyond the initial lodgepole pine stage, or that other types of forests persisted on the ridges possibly throughout or at least during the latter part of the glacial period (Hansen 1939c, 1940b). In the Black Diamond bog lodgepole pine maintains a percentage of 70 or more in the lower five levels. It decreases sharply from 70 per cent at 5 meters to 26 per cent at 4.5 meters and continues to decrease with minor fluctuation toward the surface. In the other bog lodgepole pine shows an immediate decrease from the bottom upward to only 8 per cent at 5.75 meters, from which level it is recorded in negligible proportions. The edaphic conditions were probably less favorable for this species in the vicinity of the more northern bog, because of the extensive floodplain area afforded by the numerous streams near their mouths. The well drained, gravelly terrain adjacent to the Black Diamond bog was more favorable for its persistence for a longer period of time. This is further suggested by the greater abundance of lowland white fir and Sitka spruce recorded in the lower strata of the Sedro Woolley bog (figs. 1, 2). Western white pine also diminishes upward in the profiles of both bogs, although it is more abundant near the bottom of the southern bog. This fact is also probably to be correlated with more ideal edaphic conditions in that vicinity.

Douglas fir and western hemlock are sparsely represented in the lower levels of both bogs, but the former abruptly increases inversely with the decrease of lodgepole pine (figs. 1, 2). In the Black Diamond bog Douglas fir is recorded as only 1 per cent in the lower three horizons and then sharply increases to 50 per cent at 4.75 meters. A more gradual increase is recorded in the other bog, from 5 per cent at the bottom to 62 per cent at 6.25 meters. In the former Douglas fir remains constant with minor fluctuation to 2 meters, where it attains 60 per cent. It reaches its maximum of 63 per cent at 3.75 meters, and then gradually declines from 2 meters to 33 per cent at the top. The Sedro Woolley profile shows that it likewise remained generally constant to 4.5 meters where 60 per cent is recorded, and then diminishes to 18 per cent at 1.75 meters. Again it remains more or less static to 0.25 meter, then decreases to only 10 per cent at the surface. This last decline may be the result of fire or lumbering since the advent of white man.

Hemlock has a lower gradient of increase in the pollen profiles and does not reach its maximum until later than Douglas fir, continuing to increase long after the latter had attained its peak (figs. 1, 2). Hemlock supersedes Douglas fir at 1.25 meters in the Black Diamond bog, and in the other at 2.75 meters. The maximum is reached at the surface in both bogs where 54 and 61 per cent respectively are recorded. In the Sedro Woolley bog hemlock remains predominant to the surface after it supersedes Douglas fir, while in the other both species remain more or less equal except at the surface, where hemlock exceeds Douglas fir by 21 per cent. The increase at the surface may be relative. It would be difficult to estimate the effects of a fire on the Black Diamond bog a decade or so ago. This successional relationship between Douglas fir and western hemlock suggested by the present study further substantiates similar results obtained from other peat profiles in the Puget lowland. It also strengthens the evidence that Douglas fir is a subclimax species, which has persisted as one of the chief dominants in the hemlock-cedar climax since it replaced the initial postglacial forest of lodgepole and western white pine.

Sitka spruce pollen is present in all levels of both bogs. It shows little fluctuation throughout the Black Diamond profile, ranging from 1 to 6 per cent with the higher proportions in the lower half. In the other it plays a more important part, being recorded as high as 17 per cent at 1.75 meters. The higher proportions occur in the upper half of the profile. Fir, which consists chiefly of lowland white fir, is more abundant in the Sedro Woolley bog, being best represented in the lower half of the profile and attaining its maximum of 17 per cent at 3.5 meters. In the other its maximum is 11 per cent at 0.5 meter, and it is consistently low throughout the spectrum. As was previously stated, the extensive lowland area in the vicinity of Sedro Woolley is perhaps responsible for the greater abundance of spruce and fir pollen in that peat deposit. Sitka spruce is one of the chief dominants in the hemlock-spruce climax forest in the fog belt along the Pacific Ocean. Broadleaf trees are best represented by alder, and willow and maple are recorded sporadically. Because of their local occurrence these species are probably not indicators of forest succession. Sedge, cattail, waterlily, and ericads are represented in varying quantities and mark the progression of hydrarch succession in the bog itself.

CLIMATIC CONSIDERATIONS

In several earlier papers on pollen analysis of Pacific northwest bogs, the author tentatively suggested a rather complex interpretation of postglacial climate. With the study of additional pollen profiles in this region, a more intensive study of literature dealing with the characteristics, requirements, and distribution of northwest conifers, and observation of them in the field, the conclusion has been reached that the climate has not been the most important factor concerned with postglacial forest succession. Forest succession east of the Cascades may have been influenced more by climate than that in the Puget lowland. Tolerance of shade, longevity, amount and frequency of seed production and age at initial seed production, retention of viability, ability of seed to survive fire, rate of growth, size, adaptability, susceptibility to disease, ability to withstand wind and fire, soil requirements, depth of root system, are some of the characteristics that in their interplay and compromise with one another in the same and different species have largely influenced forest succession. Tolerance of shade, longevity, age at initial seed production, and recovery after extensive fire are perhaps the most important. The present geographic and climatic ranges of the species concerned do not seem to be adequate criteria upon which to base interpretation of climatic trends from pollen profiles. The presence of a species in several regions may reflect different climates, depending upon the ecological relations of its associates. Also, a species may respond differently in areas of similar climate when associated with different species, or edaphic and topographic conditions. It would seem logical to assume that the optimum climate for a species prevails in a region where it makes its greatest sustained growth. Competition, however, may prevent its maximum development in an area of optimum climate, while lack of competition may permit its greater development in a region with less favorable climate. It is realized that all groups of environmental factors, namely physiographic, edaphic, climatic, and biotic, form an intangible, interrelated complex, each factor modifying the effect of the others. Not only may the limiting factor belong to any group, but other factors may assume the limiting role if the balance is altered.

In the hemlock-cedar climax of the Puget Sound basin, intolerance of Douglas fir seedlings for shade is perhaps the principal cause of the subclimax status of this species. Aggressiveness in invading recent burns and cutovers has enabled it to persist as one of the chief dominants during most of postglacial time. Judd (1915) stated that Douglas fir exists in the Puget Sound region only as a temporary type, which would have vanished long ago if it had not been for the effects of holocaustic fires. A parallel situation exists in northern Idaho, where western white pine likewise has been able to maintain itself in a region normally forested with a climax consisting of western hemlock, western red cedar, and lowland white fir (Hubermann 1935). A pollen profile from this region indicates that this has been true for a large portion of postglacial time (Hansen 1939a).

The pioneer invasion by lodgepole pine may have been partly due to climate and largely due to unstable edaphic and physiographic conditions. The characteristics of lodgepole pine are such that it thrives in a wider range of ecological conditions than other Pacific northwest conifers, which indicates that it can survive in a vacillating environment. Two traits, however, that have prevented it from retaining its initial predominance in the Puget lowland are its intolerance of shade and its relatively short life. In a static environment it is unable to compete with the more tolerant and longer-lived Douglas fir which thrives almost as readily in a sterile soil. The pioneer invasion of deglaciated terrain is attributed to its glacial existence near the ice-front, its early and prolific seed production, retention of seed viability, and ability to germinate in sterile mineral soil left in the wake of the retreating ice. Lodgepole pine produces seed as early as six years, and so can migrate and re-establish itself readily under changing edaphic and physiographic conditions. A tree needing 25 years or more to produce seed would be at a disadvantage before an oscillating ice-front, because it might not reach this period before a radical change in ice-position, drainage, deposition, erosion, or inundation of site destroyed it. Douglas fir and western hemlock would be unable to compete with lodgepole pine because of their greater age before producing seed. As the ice retreated farther and its wasting no longer created unstable edaphic and physiographic conditions, these and less aggressive species gained a foothold. With the moderated and more static conditions, lodgepole was no longer able to compete with the longer-lived and more tolerant Douglas fir, and was replaced. The latter would have been replaced in turn by the more tolerant hemlock and red cedar if forest succession were not periodically interrupted by fire, which caused a reversion to the subclimax type. If we assume that 500 years are necessary for a Douglas fir forest to be converted to the climax type, forest succession must have been interrupted many times during the postglacial time elapsed since the invasion of the first Douglas fir.

While it may be assumed that forest succession progresses under a static climate, nevertheless there probably have been climatic trends during the estimated 25,000 years since deglaciation. The proximity of the ice would in itself afford a cooler climate, because melting ice absorbs considerable heat.

Winds blowing off the ice may have failed to lose their moisture. On the other hand the cooling effects upon the ocean-borne air currents may have caused the latter to lose moisture. The pioneer forests suggest an initial cool and damp climate. The writer believes that it was dryer than the present humid climate. The existence of lodgepole pine in the wet climate along the Pacific Coast may be due to lack of competition by other species that cannot withstand the constant winds and sand-shear, rather than to a hydrophilic nature. The increase of Douglas fir followed by that of hemlock suggests an increase in humidity and temperature to a maximum which may persist to the present. A decrease in humidity in the latter part of the postglacial period is suggested by a sharp decline in Sitka spruce from a high maximum recorded in a pollen profile in southwestern British Columbia, about 60 miles northwest of Sedro Woolley.

The whole problem seems to resolve itself into the question of (1) what degree of species fluctuation in a pollen profile indicates a change in forest composition, and (2) to what extent does a change in the forest composition justify an interpreted climatic trend.

SUMMARY

Postglacial forest succession in the Puget Sound basin evidenced by pollen studies of two post-Vashon bogs about 100 miles apart corroborates the evidence of previous analyses of other peat deposits in the same region.

The pioneer forests consisted chiefly of lodgepole and western white pine. These were replaced rather abruptly by Douglas fir, which was followed by a more gradual increase of western hemlock. In areas adjacent to the Sedro Woolley bog hemlock eventually superseded the former and retained its predominance to the present. In the vicinity of the other peat deposit, Douglas fir and hemlock have remained generally equal as indicated in the upper levels.

Notwithstanding the evidence that forest succession in the Puget Sound basin is largely controlled by non-climatic factors, the author believes there have been several climatic trends, even though slight. The initial climate was perhaps cooler and dryer than the present humid, microthermal type. This was succeeded by an increase in humidity with some warming. The maximum of the latter trend may persist to the present, as there is no indication in the pollen profiles of further change.

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THE GENUS ORCUTTIA

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The knowledge of *Orcuttia*, a peculiar genus of grasses native to California, until quite recently has been derived from an exceedingly small number of diverse collections from widely separated localities. During the past few years, I have had the opportunity of studying in their native habitat all forms of *Orcuttia* except one. In view of the extremely scanty records previously available to botanists, it seems desirable to place on record the results of these studies.

In 1886 *Orcuttia californica* was discovered by C. R. Orcutt on the coast of Baja California. The plant was recognized by Vasey[1] as representing a genus not previously described and was named for the collector. A collection made in the Sacramento Valley by E. L. Greene in 1890 proved to belong to the same genus but differed so markedly from the Orcutt specimens in certain respects that it was regarded as a distinct species and named, also by Vasey, *Orcuttia Greenei*. For a number of years thereafter, there is no further record of the finding of either of these species. A third collection, made in Shasta County, California, by Miss Alice Eastwood in 1912, was referred at first to *O. californica* but was later recognized as distinct and named *Orcuttia tenuis* by A. S. Hitchcock in 1934. It is rather remarkable that the first three collections of the genus should represent three different species.

It was not until detailed studies of the neglected flora of the Great Valley of California were undertaken that the distribution and ecology of *Orcuttia* became fairly well known. The occurrence of *O. californica* in the Great Valley appears to have been first noted by Klyver[2] in connection with an ecologic study of a transect of the Sierra Nevada in Fresno County. In 1935 I found a plant in Stanislaus and Merced Counties which was described as *O. inaequalis*.[3] Further study has indicated that *O. inaequalis* is merely a geographically segregated variant of *O. californica*. In 1936 more extended field observations established the general distribution of that species in the San Joaquin Valley and also led to the rediscovery in the same region of *O. Greenei*, which had remained unknown since the time of its first collection. In addition, *O. tenuis* was again found in Shasta County, and a fourth species, previously unknown, was collected in Stanislaus County.

The grasses are generally thought to be exceptionally good subjects for herbarium study, because there is less distortion of the tissues in drying than in most groups of plants. However, even if the structural features could be perfectly preserved, proper evaluation of these features would not be obtained by examination of dried specimens alone. Questions such as the following would still need to be answered: Which differences among individual plants are directly due to nutrition, and which are independent of environment? In what respects does the plant change as it approaches maturity? When two or more closely related forms occur at the same locality, do they appear genetically distinct, or are they mixed in the same colonies in such a manner as to suggest common parentage? A collector may select plants which illustrate extremes of variation and unintentionally overlook intermediate states. In such cases, field study is needed to demonstrate the existence and the relative frequency of intermediates.

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[1] West Am. Sci. **3**: 4–6. 1886.

[2] Ecology **12**: 1–17. 1931.

[3] Hoover, R. F., Notes on California grasses. Madroño **3**: 227–230. 1936.

Study of the plants as they grow has tended to minimize the importance of certain differences which have been regarded as specific characters, but at the same time has shown that definite recognizable units actually exist in *Orcuttia*. Sufficient material has been available so that in no instance has it been necessary to define a species on the basis of one collection only or of collections made during a single year. The possibility of confusing seasonal variations with constant entities is thus avoided. The amount of pubescence, which was one of the characters used by Hitchcock[4] as a means of distinguishing species in this genus, is found to be variable among plants which are otherwise identical and therefore is of little significance. Readily recognizable species in this genus are distinguished principally by the arrangement of the spikelets and the nature of the lemma teeth. Other features are often of some importance, but it is necessary to exercise caution in distinguishing between specific differences and individual variation.

The ecological relationships of *Orcuttia* are extremely interesting and offer some puzzling problems for the attention of plant physiologists. All the species occupy the same sort of habitat, growing in clay soil of depressions, popularly called "hog-wallows," which are filled with water during the rainy season but become dry in early summer. The genus occurs most extensively on the east side of the Great Valley of California (Sacramento and San Joaquin Valleys) but extends southward at widely separated localities into northern Baja California. In the Great Valley two of the species are rather common along a narrow strip near the border of the Sierra Nevada foothills. Although numerous "hog-wallow" depressions similar to those inhabited by *Orcuttia* are frequent throughout the width of the valley, no species of *Orcuttia* has been found more than a few miles from the eastern margin. Two possibilities for this peculiar sort of distribution can be suggested. It has been observed that *Orcuttia* occurs nearly always in areas of red soil, chiefly of the San Joaquin series. Assuming that the red color indicates the presence of a large amount of iron, it seems plausible that these grasses may be more sensitive to a deficiency of that element than are most plants. Another explanation is suggested by the fact that the soil of extensive areas in the Great Valley, except near the eastern margin, contains large amounts of soluble minerals or "alkali." The absence of all species of *Orcuttia* from such areas indicates that these plants may be unable to tolerate either some particular substance or a concentrated soil solution of any sort.

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[4] Manual of the grasses of the United States. 1935.

All species of *Orcuttia* reach anthesis in May, when the soil where they grow is still moist but rapidly drying, and bear mature fruit in June and July, after the soil has become dry and hard. The flowers begin to develop at a time when the associated species of *Downingia*, *Allocarya*, and *Mimulus* have for the most part already come to maturity and when *Pogogyne*, *Boisduvalia*, and *Navarretia* are in full flower. The perennial *Eryngium Vaseyi*, which reaches complete maturity even later in the summer, is often the only plant associated with *Orcuttia* and actively growing at the same period, but such annuals as *Cyperus acuminatus* and *Bergia texana* are sometimes components of the same plant society.

Orcuttia tenuis and at least some forms of *O. californica* tend to produce long slender ribbon-like juvenile leaves before the development of the stems. The actual development of such floating leaves, however, depends to a large degree on environmental conditions and is therefore not seen in all specimens. After the soil of the "hog-wallow" depressions has become quite dry, *Orcuttia* develops a hygroscopic viscid secretion having a characteristic odor. This secretion is evidently found in all forms of the genus but is rather sparingly produced in some. The amount of the secretion appears to vary also with the weather, being less noticeable on cool cloudy days. This viscid fluid probably serves to prevent excessive water loss during the development of the fruit and because of its hygroscopic nature may even serve to supply the plant with water from the atmosphere.

The species of *Orcuttia* are, generally speaking, very easily exterminated by the operations of agriculture. With the apparent exception of *O. pilosa*, plowing of the ground where they occur usually prevents the reappearance of these plants in following years. It has been customary in plowing grain fields to pass over depressions which are filled with water for several months, since grain would not grow in such spots. This practice has caused the preservation of *O. Greenei* and *O. californica* at many localities in the San Joaquin Valley. Summer irrigation, however, effectively exterminates these species. With the extensive replacement of wheat and barley by other crops requiring more intensive cultivation, the final disappearance of *Orcuttia* from its native habitat must soon take place.

The phylogeny of *Orcuttia* is obscure. There is an obvious relationship to *Neostapfia*, a very rare monotypic Californian genus which grows in similar situations, often in association with *Orcuttia*. *Neostapfia* is viscid like *Orcuttia* and has the same distinctive odor. There is no clear indication that any other genus of grasses is closely related to these two genera. It is generally agreed that they are members of the tribe *Festuceae*. Because of its unbranched inflorescence and vernal-pool habitat, I am inclined to believe that *Pleuropogon* is involved in the ancestry of *Orcuttia* and *Neostapfia*, but it is at present impossible to follow the course of evolutionary development in this group of genera. In the spicate inflorescence there is a superficial resemblance to *Sesleria*, an exclusively Old-World genus of perennials, which does not appear likely to be directly related to *Orcuttia*. The striking similarity between *Orcuttia* and *Neostapfia* and the characters of *O. Greenei* indicate the fallacy of classifying *Orcuttia* with such xerophytic genera as *Pappophorum*, in which the lemmas are parted into several awns, although some authors have regarded the awn-like lemma-teeth of *O. californica* as evidence of relationship to such genera. *Orcuttia* is peculiar in that not only the fruit itself but also the florets and the spikelets are persistent after maturity. The fruit is therefore not liberated until the entire plant disintegrates during the following rainy season. This remarkable feature may be regarded as an indication of highly advanced phylogenetic position.

It has been possible to examine material representing all known collections of *Orcuttia* with the exception of the type of *O. Greenei*, of which I have seen a photograph. A few collections were made by the writer to show some biological feature, such as the long juvenile leaves, and are not represented by a full series of specimens. All other known collections of the genus are cited in this article. The material cited is preserved in the following herbaria: California Academy of Sciences (CA), Dudley Herbarium, Stanford University (S), University of California (UC).

ORCUTTIA Vasey, West Am. Sci. **3**: 4. 1886. Annuals with fibrous roots. Plants from pilose throughout to nearly glabrous, at maturity viscid and with a characteristic odor suggesting that of lemons. Stems tufted, fragile at the nodes. Leaves differentiated into sheath and blade but with ligule represented only by a row of hairs, the blades involute in age. Inflorescence spicate. Spikelets compressed, several-flowered, persistent in fruit and the rachilla not disarticulating. Glumes cleft into 2–5 acute teeth or sometimes acute and entire. Lemma with about 11–15 veins, with 5–9 acute or awn-like teeth at apex. Palea with 2 green keels terminating below the obtuse or somewhat three-lobed apex. Each cell of anther with a minute papilla at the base and a short incurved point at apex. Caryopsis small, yellowish, the embryo extending almost the entire length along one side.

TYPE SPECIES: *Orcuttia californica* Vasey.

KEY TO THE SPECIES AND VARIETIES

Spikelets spirally arranged, evenly distributed around the axis; lemma with 5 to 9 very short teeth at apex .... 1. *O. Greenei*.

Spikelets attached alternately on opposite sides of the axis, thus in two rows; lemma with 5 rather long teeth.

Spike 2 to 5 cm. long, the axis usually not strictly erect; spikelets ascending, tending to grow toward one side, thus obscuring the two-ranked arrangement; teeth of lemma unequal, the middle tooth longest.

Spikelets borne only on upper third or fourth of stem; glumes 2 to 5 mm. long; lemma 3 to 6 mm. long.

Plant rather sparingly pilose, light green; spikelets 4 to 10, not crowded; (fruit unknown) .... 2. *O. californica.*

Plant conspicuously pilose, grayish; spikelets 7 to 15, the upper densely crowded; caryopsis 1.3 to 1.75 mm. long.
2a. *O. californica* var. *inaequalis.*

Spikelets often extending as low as middle of stem; glumes 6 to 10 mm. long; lemma 6 to 8 mm. long; caryopsis 2.5 mm. long .... 2b. *O. californica* var. *viscida.*

Spike 5 to 10 cm. long, the axis strictly erect; spikelets usually appressed to the axis, obviously two-ranked; lateral teeth of lemma equalling the median tooth.

Stems rather stout; leaf-blades when unrolled 2 to 6 mm. wide at widest point; upper spikelets densely crowded, all except the lowermost many-flowered.
3. *O. pilosa.*

Stems slender; leaf-blades when unrolled 1 to 2 mm. wide at widest point; spikelets not crowded, all except the uppermost few-flowered .... 4. *O. tenuis.*

1. ORCUTTIA GREENEI Vasey, Bot. Gaz. **16**: 146. 1891. Plant not producing long juvenile basal leaves, only slightly glandular at maturity; stems 5 to 30 cm. long, erect or decumbent at base; nodes hairy, often purplish, excessively fragile in fresh plants; leaves more or less hairy throughout or only on the upper surface of the blades, the sheaths shorter than the internodes at maturity; spike 2 to 9 cm. long, enlarged toward apex; spikelets spirally arranged (not two-ranked), the lowest hardly longer than the internodes, the upper congested, with 5 to 15 flowers; glumes 3 to 5 mm. long, toothed or subentire at apex; lemma 5 to 7 mm. long, rather sparingly hairy, broadest below the middle, obliquely truncate and with 2 to 4 very short teeth on either side of the prominent apical point; palea obtusely three-lobed at apex, the veins terminating in the sinuses; anthers 3 to 3.5 mm. long; caryopsis 2.25 to 2.5 mm. long, very minutely but rather conspicuously roughened.

Great Valley of California, near the eastern margin from Tehama County to Tulare County.

CALIFORNIA—TEHAMA CO.: near Vina, *Hoover 2249* (UC). BUTTE CO.: near Chico, 1890, *Greene* (photograph of TYPE, UC). SAN JOAQUIN CO.: Farmington, *Hoover 1302* (CA); 2 miles east of Escalon, *Hoover 1288* (S). STANISLAUS CO.: Paulsell, *Hoover 2441* (UC); 3 miles northwest of Waterford, *Hoover 1582* (CA), *2476* (S); 12 miles east of Waterford, *Hoover 1240* (CA, UC), *3625* (S). MERCED CO.: 2 miles northeast of Planada, *Hoover 2303* (S, UC); 5 miles southeast of Le Grand, *Hoover 1255* (CA). MADERA CO.: 8 miles north of Madera, *Hoover 1251* (CA, UC). FRESNO CO.: 5 miles east of Clovis, *Hoover 2317* (S, UC); 4 miles north of Sanger, *Hoover 1261* (CA). TULARE CO.: Woodlake, *Hoover 1287* (CA).

This species appears to be the commonest of the genus and is remarkably uniform in its characters. Together with species such as *Limnanthes rosea, Downingia ornatissima,* and *D. mirabilis,* it belongs to a well defined group of endemic plants of the vernal pools in the Great Valley of California. The number of lemma-teeth has no taxonomic significance, as it varies within a single spikelet.

From the above citations, it will be noticed that *O. Greenei* apparently occurs in two separate areas, the upper Sacramento Valley and the eastern margin of the San Joaquin Valley. Study of the geographical distribution of other plants occurring in the same region indicates that the range of this species should be continuous. In all probability it has been overlooked by collectors in the lower Sacramento Valley, or perhaps it has already been exterminated in that region.

2. ORCUTTIA CALIFORNICA Vasey, West Am. Sci. **3**: 4. 1886. Plant from sparingly to moderately pilose, evidently without long basal leaves in the typical form; stems 10–50, spreading or ascending, 5–15 cm. long; sheaths of leaves mostly longer than the internodes and concealing the nodes (mature plants not seen); spikes 2–5 cm. long; spikelets alternate on opposite sides of the axis, ascending, tending to be all directed to one side, rather few (4–10), the lower not overlapping and even the upper not densely crowded, with about 4 to 12 flowers; glumes 2 to 4 mm. long; lemma sparsely hairy or nearly glabrous, 4 to 5 mm. long, parted above the middle into 5 subulate teeth, the middle tooth slightly exceeding the lateral; anthers 2 to 2.75 mm. long; fruit unknown.

Coastal region from Riverside County, California, to northern Baja California.

CALIFORNIA—RIVERSIDE CO.: Menifee Valley, *Munz & Johnston 5375* (CA, S, UC). BAJA CALIFORNIA: near San Quentin Bay, *Orcutt 1139* (type collection, S, UC).

The species on which the genus was originally based is the only one which is still very poorly known in the typical form. I suspect that it occurs at other localities in the south but has been overlooked, just as the following variety in the San Joaquin Valley was overlooked for many years.

2a. ORCUTTIA CALIFORNICA Vasey var. **inaequalis** Hoover, comb. nov. *O. inaequalis* Hoover, Madroño **3**: 229. 1936. Plant grayish, rather densely pilose, producing long basal floating leaves which usually disappear at maturity; sheaths of leaves either longer or shorter than internodes; stems from 1 to about 40, erect to spreading, 5–30 cm. long; spikelets 7–15, all except the lowermost densely crowded, with from 4 to as many as 30 flowers; glumes 2–5 mm. long; lemmas hairy, 3–6 mm. long, the teeth conspicuously unequal, awn-tipped, the middle tooth longest; caryopsis about 1.3–1.75 mm. long.

San Joaquin Valley of California, near the eastern margin from Stanislaus County to Tulare County.

CALIFORNIA—STANISLAUS CO.: 3 miles northwest of Waterford, *Hoover 1230* (CA); Montpellier, *Hoover 582* (TYPE, UC), *690* (CA, S, UC), *2599* (CA). MERCED CO.: Ryer, *Hoover 1256* (CA); 2 miles northeast of Planada, *Hoover 2306* (S, UC). MADERA CO.: 8 miles north of Madera, *Hoover 1252* (CA, UC). FRESNO CO.: near Lane's Bridge, *Klyver 1006* (S); 3 miles west of Orange Cove, *Hoover 1273* (CA). TULARE CO.: North Woodlake, *Hoover 1280* (CA).

The observed differences between this plant and typical *O. californica* are not sharply defined, but it is always possible to distinguish the two. This fact, together with the wide geographical separation, makes it advisable to recognize a variety rather than treating the two forms as a unit.

The variety *inaequalis* is characterized by some striking variations in habit. Although one habit form usually prevails in any given locality, each colony shows sufficient variation to prevent any formal classification on that basis. The most common form in Stanislaus County has short ascending stems. In Madera County a decumbent or prostrate phase is more frequent, while in Tulare County most of the plants are tall and erect. Rarely the spikes are branched.

2b. ORCUTTIA CALIFORNICA Vasey var. **viscida** Hoover, var. nov. Plant tending to produce long juvenile leaves, becoming very viscid; spikes 2–5 cm. long, the spikelets 5–15, more strictly ascending than in var. *inaequalis* and borne farther down on the stem; glumes 6–10 mm. long; lemma 6–8 mm. long, with unequal awned teeth; caryopsis 2–2.5 mm. long.

Planta viscidissima; lemmatibus 6–8 mm. longis, dentibus aristatis; caryopside 2–2.5 mm. longa.

Near the Sierra Nevada foothills in Sacramento County, California.

CALIFORNIA—SACRAMENTO CO.: 2 miles southeast of Orangevale, *Carter 1193* (UC); 7 miles south of Folsom, *Hoover 3709* (UC, TYPE, S).

The long lemmas with awned teeth give to var. *viscida* a distinctive aspect. In view of the geographical proximity of this variety to var. *inaequalis*, the differences between the two show a remarkable contrast to the similarities between var. *inaequalis* and typical *O. californica*. These differences do not seem sufficiently well defined, however, to warrant specific segregation, especially while the size of the caryopsis in typical *O. californica* is not yet known.

3. **Orcuttia pilosa** Hoover, sp. nov. Plant often producing long basal leaves which early disappear, very viscid at maturity, pilose throughout but the backs of the leaves nearly glabrous; stems 4–50, erect but decumbent at base, 5–20 cm. tall, usually in dense tufts; spikes 5–10 cm. long, restricted to the upper half or third of the taller stems but extending nearly to the base of the shortest; spikelets 8–18, two-ranked, strictly erect or slightly curved outward, the upper densely crowded, about 10–40-flowered; glumes about 3 mm. long, irregularly 3–5-toothed; lemmas 4–5 mm. long, parted above the middle into 5 equal teeth, the teeth slightly awn-tipped or merely acute; anthers 2.5–3 mm. long; caryopsis 1.75–2 mm. long.

Planta omnino pilosa, in maturitate viscidissima; culmis 4–50, erectis sed basi decumbentibus, 5–20 cm. altis; spicis 5–10 cm. longis; spiculis 8–18, biseriatis, ca. 10–40 floribus, superioribus dense congestis; glumis ca. 3 mm. longis; lemmatibus 4–5 mm. longis, dentibus aequalibus; antheris 2.5–3 mm. longis; caryopside 1.75–2 mm. longa.

East side of the San Joaquin Valley of California from Stanislaus County to Madera County.

CALIFORNIA—STANISLAUS CO.: 12 miles east of Waterford, *Hoover 1298* (CA), *3624* (UC, TYPE, S). MADERA CO.: 3 miles from Madera on Northfork road, 1938, *Wagnon* (UC); Crocker-Hoffman Ranch, 1938, *Wagnon* (UC).

In general aspect this very rare species is quite different from *O. tenuis*, which it closely resembles in structural details. As long as *O. pilosa* had been found only at one locality in Stanislaus County, there was reason to suspect that it was merely a robust form of *O. tenuis*, and a few specimens were distributed by the writer under that name, but the occurrence of exactly the same form in Madera County indicates that it is a well defined and constant entity and therefore worthy of taxonomic recognition. This conclusion is supported by geographical considerations. Within their widely separated ranges, *O. tenuis* and *O. pilosa* vary only within definite limits and never simulate each other in appearance, although it is difficult to find an entirely convincing morphologic basis for their segregation.

4. ORCUTTIA TENUIS A. S. Hitchcock, Am. Jour. Bot. **21**: 131. 1934. Plant under favorable conditions producing long floating juvenile leaves, becoming very viscid at maturity, 5–15 cm. tall; stems 1–18, slender, strictly erect or when crowded decumbent at base; leaves thinly pilose throughout or sometimes only on the upper surface of the blades; spike 5–9 cm. long, extending usually below the middle of the stem, often nearly to the base; spikelets 6–12, not crowded, strictly erect, sparsely pilose or sometimes glabrous, with 2–10 flowers (all except the uppermost few-flowered), the lower distant; glumes 3–5 mm. long, with 2–5 teeth at apex; lemma 4.5–6 mm. long, parted above the middle into 5 equal awn-tipped teeth; anthers 2.75–3.5 mm. long; fruit unknown.

Shasta and Tehama Counties, California, east of the Sacramento River.

CALIFORNIA—SHASTA CO.: Goose Valley, *Eastwood 1013* (type collection, CA, UC); 5 miles east of Redding, *Hoover 2268* (S, UC); 4 miles north of Anderson, *Hoover 1210* (CA, UC). TEHAMA CO.: volcanic plateau northeast of Red Bluff, *Hoover 4097* (CA, S, UC).

Orcuttia tenuis comes into flower somewhat earlier than the species occurring farther south in the Great Valley, thus reversing the order of development observed in most genera. Under the original description, the habitat of *O. tenuis* was said to be "open sandy soil," but that appears to be an error. The species always grows in beds of vernal pools, so far as I have observed. The slender erect stems, bearing spikelets nearly to the base, are distinctive.

NORTH AMERICAN RANUNCULI—I

LYMAN BENSON

The following series of articles[1] is a presentation of data on the North American *Ranunculi* occurring north of the Mexican boundary of the United States. It consists of detailed geographical ranges, determination of type specimens, new names and new combinations, descriptions of varieties not included in Abrams Illustrated Flora of the Pacific States **2**: 1940 with the opposed characters of the typical species, and citation of a few significant specimens for misunderstood or rare species. In order to show the bases for reorganization of species and varieties and to facilitate reference of plants to the proper categories, keys are included.

The first paper deals with the first seven species and a complex of varieties of the subgenus *Euranunculus*, section *Chrysanthe*, as delimited by Benson; cf. Am. Jour. Bot. **23**: 26–33, 169–176. 1936. **27**: 799–807. 1940.

SECT. 1. CHRYSANTHE (SPACH) L. BENSON

KEY TO THE SPECIES

Achene beaks not over 2 mm. long, regularly-curved or hooked.

Fruiting receptacle not more than 2.5 times the length in anthesis; head of achenes hemispherical or globose.

Petals large and conspicuous, 6–18 mm. long, at least twice as long as the sepals.

Stems rooting at the nodes .... 3. *R. repens.*

Stems never rooting adventitiously (except at some subterranean nodes near the stem base in *R. californicus* var. *cuneatus.*

Stem base a conspicuous, bulb-like, subterranean thickening 6–7 mm. long by 10–13 mm. in diameter .... 4. *R. bulbosus.*

Stem base not bulbous.

Sepals spreading; petals clawless or nearly so; stems unbranched in the first 2–3 dm.

Achene beak 0.3–0.6 mm. long .... 1. *R. acris.*

Achene beak 1.2–1.7 mm. long .... 2. *R. acriformis.*

Sepals reflexed at or below the middles (except in *R. occidentalis* var. *Turneri*); petals with claws; stems usually branched in the first 2 dm.

Achenes 1–3 or rarely 3.5 mm. long.

Petals 5–6 or rarely 7–9 or 12, the blades 1–2 or rarely 2.5 times as long as broad .... 5. *R. occidentalis.*

Petals 9–16 or 26, rarely fewer, the blades 2–2.5 times as long as broad. 6. *R. californicus.*

Achenes 3.5 or usually 4–5 mm. long; petal blades 1–2 or, in a variety, 2–2.5 times as long as broad .... 7. *R. canus.*

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[1] This is the first of a series of five articles dealing with the taxonomy of North American *Ranunculi.*

Petals minute, 4 mm. long or less, or 4–6 mm. in a rare southern Colorado variety of *R. Bongardii;* petals and sepals of about equal length.

Receptacle conspicuously hairy, usually 3–4 mm. long in fruit.

Nectary scale forming a pocket one-fourth the size of the petal; stem base bulbous, the plant perennial; herbage hirsute; achenes finely reticulate; cauline leaves simple, parted and toothed, the teeth obtuse .... 8. *R. recurvatus.*

Nectary scale not forming a pocket, free laterally; stem base unknown, the plant perhaps annual; herbage glabrous; achenes somewhat rough-reticulate (on a much larger pattern); cauline leaves pinnately 3-foliolate, the lateral parts simple or 2–3-toothed .... 10. *R. Macounii.*[2]

Receptacle glabrous; nectary scale not forming a pocket, free laterally, much less than one-fourth the size of the petal; stem base not bulbous; cauline leaves parted and lobed, the lobes acute .... 9. *R. Bongardi.*

Fruiting receptacle at least 3 times the length in anthesis, hispid; head of achenes ovoid or cylindrical.

Sepals equal to or a little shorter than the petals, the petals 3 or 5–7 mm. long; head of achenes ovoid, 7–9 mm. long; stems often rooting at the nodes. 10. *R. Macounii.*

Sepals about twice the length of the petals, the petals 2–3 mm. long; head of achenes cylindrical, 11–17 mm. long; stems never rooting adventitiously. 11. *R. pennsylvanicus.*

Achene beaks 2–4 mm. long, straight or bent but not regularly-curved and not hooked at the tips for more than 0.1 mm. (cf. also *R. occidentalis* vars. *dissectus* and *Howellii*); receptacle hispid.

Petals 8–18; roots of the main fascicle all alike (*R. fascicularis* var. *cuneiformis* has 7–9 petals, but it has the roots of the main fascicle differentiated into two types). 12. *R. macranthus.*

Petals 5 or 6.

Roots of the main fascicle all alike, not differentiated into two types.

Sepals reflexed.

Petals 4–7 mm. broad, rarely narrower; stems usually 1.5 mm. or more in diameter (except in *R. Bloomeri,* which has usually emarginate petals).

Petals not emarginate; leaves at least sparsely hairy.

Sepals two-thirds or three fourths the length of the petals; leaflets of the radical leaves 3 or the leaves simple; plants often stoloniferous in summer. 16. *R. septentrionalis.*

Sepals half the length of the petals; leaflets of the radical leaves 3–7; plants never stoloniferous .... 13. *R. orthorhynchus.*

Petals usually emarginate; leaves glabrous, shining .... 14. *R. Bloomeri.*

Petals 2–3 or rarely 4 mm. broad; stems 0.7–1.5 or 2 mm. in diameter; plant subglabrous .... 15. *R. carolinianus.*

Sepals spreading (rarely reflexed in *R. septentrionalis,* as shown in the key above).

Sepals two-thirds or three-fourths the length of the petals; plant often stoloniferous in summer; achene keel well-marked; plant usually, but not always, either subglabrous or sparsely hairy .... 16. *R. septentrionalis.*

Sepals half the length of the petals; plant never stoloniferous; achene keel obscure; plant always markedly hairy .... 17. *R. hispidus.*

Roots of the main fascicle of two kinds, some filiform (about 0.5 mm. in diameter) and some fleshy or tuberous and 1–5 mm. in diameter .... 18. *R. fascicularis.*

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[2] A reduced form occurring along Peace River.

1. **Ranunculus acris** L. Sp. Pl. 554. 1753. Pastures, meadows, and roadsides at low elevations or up to 1,000 or 1,300 meters elevation in the Western mountains; Europe; naturalized in North America at Kodiak and King Cove, Alaska and from British Columbia to Saskatchewan and to Western Washington, Oregon (Salem, Brooks, and Union), and Missouri; Minnesota and northern Illinois to Labrador and New England and south on the Atlantic coastal plain to North Carolina; Greenland and Iceland.

Type collection: "Habitat in Europae *pratis, pascuis."*

A European form called *Ranunculus acris* var. *Stevenii* (Andrz.) Lange has been distinguished by its less-dissected leaves with broadly oblanceolate or more-or-less cuneate segments. This form occurs in the Craigmyle District, Alberta, and from Quebec to Newfoundland, Nova Scotia, New England, and New York, and is occasional elsewhere. According to the viewpoint of the writer, the characters of this plant do not entitle it to recognition as a variety.

According to a note by Ora Parker Phelps, Rhodora **21**: 208. 1919, *Ranunculus Boraeanus* Jordan, Obs. Pl. Crit. (6) 19. 1847, a Central-European relative or variety of *R. acris* with finely-dissected leaves, was found in 1919 at Gansevoort, New York. It was identified by Dr. M. L. Fernald.

2. **Ranunculus acriformis** A. Gray, Proc. Am. Acad. **21**: 374. 1886. Wet meadow land at 2,000–2,500 meters elevation; reported from Alberta; Sweetwater County to Laramie County, Wyoming; Laramie River in Colorado. Plains grassland. June and July.

Type collection: "R. acris, Hook. Fl. i. 18, & Lond. Jour. Bot. vi. 66, not L.—Northern Rocky Mountains, lat. 58°, *Drummond.* Wyoming, *Parry* (distrib. as R. affinis). Wind River, *Dr. Forwood,* and near Cheyenne, *Greene.*" Hooker, l.c., cites the Drummond specimen as follows: "Banks of rivers in the central limestone district, and eastern primitive range, from Canada to lat. 58°, *Drummond.*"

Significant specimens: COLORADO: Laramie River, *Crandall* in 1891, NY, US. IOWA: Belmond, *Whited* in 1903, WSC (questionable identification).[3]

3. **Ranunculus repens** L. Sp. Pl. 554. 1753. *R. Clintonii* Beck, Bot. N. & Mid. St. 9. 1833.

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[3] The symbols used for the herbaria in which specimens are located are as follows: S, Dudley Herbarium, Stanford University; NY, New York Botanical Garden; GH, Gray Herbarium, Harvard University; US, United States National Herbarium; UW, University of Washington; T, J. W. Thompson, Seattle, Washington; WSC, Washington State College; UO, University of Oregon; WILL, Willamette University; OSC, Oregon State College; UC, University of California; J, W. L. Jepson, University of California; CA, California Academy of Sciences; SBM, Santa Barbara Museum; P, Pomona College; ISB, University of Idaho Southern Branch; UA, University of Arizona; SAC, U. S. Field Station, Sacaton, Arizona; COLO, University of Colorado Museum; F, Mr. O. A. Farwell, Lake Linden, Michigan; B, Lyman Benson, University of Arizona; MINN, University of Minnesota; MICH, University of Michigan; CORN, Cornell University; K, Kansas State College of Agriculture and Applied Science; HGr, Herbarium Greeneanum.

Stems prostrate,[4] rooting adventitiously at practically every node, 1–50 dm. long and 0.7–1.5 mm. in diameter, not fistulous, appressed-hairy in the typical form; leaf blades compound, deltoid-cordate in outline, 1.5–6 cm. long, 2–8 cm. broad, pinnate with 3 sessile or petiolulate leaflets, which are proximally cuneate and distally lobed and toothed but acute in outline, middle petiolule up to 4 cm. long, the lateral petiolules up to 2 cm. long; petals 5, 7–13 mm. long; achenes 20–25 in a subglobose head; receptacle subglobose-ovoid.

Meadows and marsh borders at low altitudes or up to 1,500 meters in the Rocky Mountains; Europe; naturalized in North America from the south coast of Alaska to coastal California as far south as Carmel River (also at Cobb Valley in Lake County, at Quincy, Bear Valley, and Pine Ridge (Fresno County) in the Sierra Nevada, and at Goose Lake); Rocky Mountain System in Custer County, Idaho and at Denver, Colorado; Quebec to Newfoundland and North Carolina. May to September.

Often a lawn weed, the prostrate habit and adventitious roots cheating the mower.

Type collections: (1) *R. repens*, "*Habitat in* Europae *cultis*." (2) *R. Clintonii*, "Hab. Banks of Canal near Rome, Oneida Co., N. Y."

Dr. M. L. Fernald, Rhodora **21**: 169. 1919, gives the following key for segregation of the varieties of *R. repens*:[5]

A. Middle leaflet of the basal leaves cuneate to subtruncate at the base: petals 5–9; stamens numerous .... B.
  B. Lobes and teeth of the leaves deltoid or obovate to oblong, obtuse or bluntish.
    Trailing or repent branches or stolons present.
      Stems and petioles distinctly pubescent.
        Pubescence appressed .... *R. repens* L.
        Pubescence wide-spreading .... Var. *villosus* Lamotte.
      Stems and petioles glabrous or nearly so .... Var. *glabratus* DC.
    Trailing or repent branches wanting .... Var. *erectus* DC.
  B. Lobes and teeth of the much-cleft leaves lanceolate to linear, acuminate. Var. *linearilobus* DC.
A. Middle leaflet of the basal leaves rounded or subcordate at the base: petals very numerous, forming a "double" flower .... Var. *plentiflorus* Fern.

R. repens var. *villosus* LaMotte is the common spreading-hirsute form of the species. On the Pacific Slope it is the dominant form, and, in fact, the typical species is uncommon or even rare (collected only as follows: Salem,

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[4] Wherever abbreviated descriptions are given under the name of the species alone they apply to the typical variety and not to the species as a whole.

[5] While the validity of the philosophy behind the use of the formal name "var. *typica*" is admitted, it is the opinion of the author that publication of formal trinomials for typical varieties is unnecessary. The long-established custom is to consider the plant described under the specific name as the typical variety within the species and to give varietal names to only the other varieties of the species.

Oregon, *J. C. Nelson 225;* Noyo, Mendocino County, California, *Duncan 181;* Alhambra, California, *Mrs. J. D. Abrams*). However, according to the viewpoint of the writer, the "var. *villosus*" is not worthy of recognition as a variety.

3A. RANUNCULUS REPENS L. var. GLABRATUS DC. Prodr. **1**: 38. 1824. Similar to but even more robust than var. *erectus* and perhaps not distinct from it; stoloniferous; stems up to 7 or 9 dm. long; leaf blades up to 10 or 11 cm. long and 13 cm. broad, petiolules as much as 2.5 cm. long; flowers in an extreme form subcymose; petals 5; receptacle and head of achenes sometimes ovoid-cylindrical.

European plant naturalized in wet places here and there from Quebec and Newfoundland to New England and New Jersey; Farmington and Salt Lake City, Utah, May to August.

The extreme form is so strikingly different from *R. repens* as to seem to be another species, but intermediates are more common than the extremes.

Type collection: None given, European.

Significant specimens (representative of the extreme form): NEWFOUNDLAND: Force le Plain, Harry's Brook, *R. B. Kennedy 336*, GH. QUEBEC: Carleton, *Collins, Fernald, & Pease* in 1904, GH. UTAH: Farmington, *M. E. Jones* in 1881, NY, *Clemens* in 1908, GH. NEW JERSEY: Closter (?), *unnamed collector* in 1861, GH. MASSACHUSETTS: Wellesley, *Gilbert* in 1894, GH; Nantucket, *Day 4* in 1900, GH; Botanic Garden of Harvard University in 1862, GH.

3B. RANUNCULUS REPENS L. var. ERECTUS DC. Prodr. **1**: 38. 1824. Growing often in shallow water of meadow or marsh land: naturalized in the Puget Sound Region and southward at scattered stations mostly near the ocean coast to Curry County, Oregon; Santa Cruz, California; occasional in Quebec and Newfoundland. May to July. Cf. L. Benson in Abrams, Ill. Fl. Pacif. St. **2**: 1940.

Type collection: None given, European.

R. repens var. *linearilobus* DC. occurs sparingly in New England. The following specimens are in the Gray Herbarium: Cutler, Maine, *Kennedy, Williams, Collins, & Fernald* in 1902; Waverly Oaks, *Gray Herbarium Local Collection*, 1894; Nantucket, Mass., *Day 13* in 1900. According to the viewpoint of the writer, this form is not worthy of recognition as a variety. The status of the plant is about the equivalent of that of *R. acris*, var. *Stevenii*, since there is only the degree of dissection of the leaves to distinguish it.

3C. RANUNCULUS REPENS L. var. PLENIFLORUS Fern. Rhodora **19**: 138. 1917. Wet ground, an occasional escape from gardens in New York, New England, and Maryland; Liberty, Kittitas County, Washington. May to July. Cf. L. Benson in Abrams, Ill. Fl. Pacif. St. **2**: 1940.

Type collection: "Frequent in old gardens, and tending to become naturalized in meadows and along roadsides, Oneida, Herkimer County, New York, May 30, 1900, J. V. Haberer, no. 1530 in Gray Herb.

"This plant is generally called in horticulture *R. repens*, var. *floreplено* but the latter name (if it can be accepted as a valid name) belongs to the double-flowered European form of *R. repens* with the bases of the leaflets cuneate to subtruncate, as in true *R. repens*, and the teeth and segments elongate and subacute to acuminate. The history of var. *pleniflorus* is obscure. It is found in old gardens and as a somewhat naturalized weed in eastern America; but such illustrations of the double-flowered *R. repens* of Europe as the writer has seen, as far back as Gerard's Herball (ed. Johnson, 1633), where the plant is figured as *Ranunculus dulcis, multiplex,* and Besler's Hortus Eystettensis (1613) where it is called *Ranunculus hortensis, multiflorus,* show the characteristically cuneate-based leaflets of *R. repens.*"

4. RANUNCULUS BULBOSUS L. Sp. Pl. 554. 1753.[6] Dry fields and roadsides at low elevations; Europe; naturalized in North America at Revelstoke, British Columbia, St. John's, Newfoundland, Shelbourne, Nova Scotia, Bingen, Washington, Salem, Oregon, Fortuna, California, Oquauka (?) Illinois, Keneewaw County, Michigan, Lake Maxinkuckee, Indiana, Knoxville, Tennessee, Red River, Louisiana, and Stumptown, West Virginia and from New York and New England to Bryan County, Georgia. May and June.

Type collections: (1) *R. bulbosus, "Habitat in* Europae *pratis, pascuis."* (2) Var. *petiolulatus,* "No. 5568. In und um Norfolk häufig." "Im Mai & Juni 1890, botanisierte ich um Norfolk." Virginia, *Krause.*

THE RANUNCULUS OCCIDENTALIS COMPLEX

The *Ranunculus occidentalis* group is perhaps only scarcely less difficult to classify than the races of dogs. There are no wholly reliable characters for segregation of the species *R. occidentalis, R. californicus,* and *R. canus,* and wherever geographic ranges meet all three species and their 10 varieties seem to cross-pollinate freely, or at least the plants in the field show abundant evidence of character recombinations. However, the large fruit of *R. canus* is fairly reliable for distinguishing it from the other two species, and the number of petals serves to segregate all but a small percentage of the plants of *R. californicus* and its three few-petaled varieties from *R. occidentalis* and its sometimes 5–8- or rarely 9–12-petaled varieties *Rattanii* and *Eisenii.* Table 1 summarizes the tendencies in these three species.

5. RANUNCULUS OCCIDENTALIS Nutt. in Torr. & Gray, Fl. N. Amer. **1**: 22. 1838. *R. occidentalis* var. *robustus* A. Gray, Proc. Am. Acad. **21**: 373. 1886. *R. tenuipes* Heller, Muhlenbergia **1**: 50. 1904. *R. occidentalis* var. *laevicaulis* Suksdorf, West Am. Sci. **15**: 58. 1906.

Stems erect or suberect, 2–7 dm. long, 1.5–3 mm. in diameter, freely branching; radical leaf blades simple, rather thick, 1.5–3.5 cm. long, 2–4.5 cm. broad, 3-parted or rarely -divided, the lobes cuneate, again lobed, the ultimate lobes usually not triangular, the sides commonly curving, proximally cordate and distally rounded or acute; petals 5 or rarely 6–8, narrowly

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[6] Two old-world varieties are distinguished from the typical one by Fernald, Rhodora **42**: 451–452. 1940.

TABLE 1

	R. occidentalis	*R. californicus*	*R. canus*
Petal Number (Fairly reliable)	5–6 or in 3 vars. sometimes 5–8 or 12.	9–16 or 26 or in 3 vars. 5 or 7–12.	5–10 or in 1 var. 10–23.
Petal Shape (Less reliable)	1.5–2 or rarely 1.1 or 2.5 times as long as broad.	2–2.5 times as long as broad.	1–2 times as long as broad; 1 var. 2–2.5.
Fruit Size (Fairly reliable)	2.5 × 2 mm. or in vars. up to 3 × 2.5 or even 3.5 × 3.3.	2–2.8 × 1.8–2.3 mm. or in 1 var. 1–2 × 1–1.5.	4–5 × 3–4.5 mm. or rarely smaller.
Achene beak (Less reliable)	1.2–1.8 mm. long or in 2 vars. 0.5–1.3; 2 vars. 1.5–2.	Usually 0.4–0.8 mm. or in 1 var. 1–1.5.	0.3–0.6 or 1 mm.
Plant Size (General tendency)	Smaller, except vars. *Eisenii, montanensis,* and *Nelsonii.*	Larger, except var. *cuneatus.*	Largest, also herbage more commonly silky-villous.
Compound leaves (General tendency)	Rare, except var. *Eisenii.*	Common, except vars. *gratus* and *cuneatus.*	Common in var. *laetus,* otherwise uncommon.

elliptic, 1.5–2 times as long as broad (claw 1–3 mm. long), 8–12 or rarely 18 mm. long, 3.5–5 or 8 mm. broad, the nectary scale glabrous, free for nearly the whole length, 0.7 mm. long, truncate; each achene obovate-discoid, 2.5 mm. long, 2 mm. dorsoventrally, 0.3–0.4 mm. laterally, glabrous, the achene beak slender, 1.2–1.8 mm. long, falcate, usually barely recurved, prolonging the ventral margin of the achene body.

Mostly beneath trees or on vernally moist prairies or hillsides; Pacific Slope from Alaska to the Umpqua River Valley, Oregon; inland along the Columbia River to west Klickitat County, Washington and The Dalles, Oregon; Port Orford, Oregon. Northwestern coniferous forest. Late April and May.

This species, *R. canus, R. californicus,* and their varieties have an abundance of connecting forms. A form with petals 15–18 mm. long by 7–8 mm. broad occurs at The Dalles and near Eugene, Oregon.

Type collections: (1) *R. occidentalis,* "Plains of the Oregon (Columbia) River, near woods, *Nuttall!* Dr. Scouler!; Sitcha, *Bongard!*" The Nuttall specimen at Columbia University (New York Botanical Garden) has been designated as a LECTOTYPE (cf. Heller, Muhlenbergia **1**: 51. 1904.) (2) Var. *robustus, R. occidentalis* A. Gray, Proc. Amer. Acad. **8**: 374. 1872, not. Nutt in 1838. "A collection of plants made in Oregon by ELIHU HALL during the summer of 1871." (3) *R. tenuipes, Heller* "No. 3935, collected June 13, 1898 at Montesano, Chehalis [Gray's Harbor] county, Washington, altitude about 200 feet." (4) Var. *laevicaulis,* "An verschiedenen Stellen mit her gewöhnlichten Form vermengt, bei Bingen, Washington, 30 März 1886 und später (Nr. 1972)," *Suksdorf.*

Significant specimens of *Ranunculus occidentalis* and its varieties: see L. Benson, Am. Jour. Bot. **23**: 28–29. 1936.

5A. RANUNCULUS OCCIDENTALIS Nutt. var. RATTANII A. Gray. Proc. Am. Acad. **21**: 373. 1886. *R. Rattanii* Howell, Fl. N. W. Am. **1**: 17. 1897.

Openly wooded hills and prairies; inner part of the seaward coast ranges from Coos and western Josephine Counties, Oregon to Mendocino and western Lake Counties, California. Borderland between the Northwestern coniferous forest and the oak woodland. April to June. Cf. L. Benson in Abrams, Ill. Fl. Pac. Sts. **2**: 1940.

The hispid achene is to be found in any of the southern varieties of *R. occidentalis*, as well as in *R. californicus* and *R. canus*. It is not necessarily a feature of var. *Rattanii* or of any other variety. This variety is rather striking in the extreme form but throughout the seaward side of the distributional range it intergrades with *R. californicus* var. *gratus*, and in the north it passes into *R. occidentalis* var. *Howellii* and in the south into the variety *Eisenii*.

Type collection: "N. California on the Klamath, Rattan." The TYPE specimen in the Gray Herbarium is labelled as follows: "Common on the Klamath, Calif. *V. Rattan*, June, 1879."

5B. RANUNCULUS OCCIDENTALIS Nutt. var. EISENII (Kell.) A. Gray. Proc. Am. Acad. **21**: 373. 1886. *R. Eisenii* Kell. Proc. Calif. Acad. **7**: 115. 1876.

Vernally moist ground in the California foothills and mountain valleys at 100–1,300 meters or up to 2,200 meters elevation in Kern County, beneath oaks (leaves simple) or in vernal meadows and rivulets (leaves compound); Weaverville; eastern Mendocino, Lake, and eastern Napa Counties; Sierra Nevada foothills and Greenhorn and Tehachapi Mountains; West Butte, Sacramento Valley. Oak woodland. Late February to May or June. Cf. L. Benson in Abrams Ill. Fl. Pacif. St. **2**: 1940.

The form of *R. occidentalis* growing from southeastern Jackson County and southwestern Klamath County, Oregon, to Shasta County, California, is intermediate between the varieties *Eisenii* and *ultramontanus*. The variety *Eisenii* intergrades freely with *R. californicus* at Healdsburg and at the south base of Mt. St. Helena, where 5-petalled and 9–16-petalled plants are found growing together. The compound-leaved forms from vernal meadows and the simple-leaved forms from oak woodland maintained their characters when transplanted by the writer to identical environments in adobe soil at Menlo Park, California. A glabrous, dissected-leaved form (L. Benson 6316) was found growing in water at Stubbs Ranch Junction north of Lower Lake, Lake County.

Type collection: cf. Proc. Calif. Acad. **7**: 89. 1876, "Dr. Eisen, of Sweden, placed in our hands for determination his plants from near Fresno, Cal." The type is unknown, and it may have been destroyed in the San Francisco earthquake and fire of 1906. However, according to Curran, Bull. Calif. Acad. **1**: 130. 1885, it disappeared much earlier. The following is her statement, "*Ranunculus Eisenii* Kellogg, Proc. Cal. Acad. vii. 115. Probably *R.* NELSONII var. TENELLUS, Gray, but the specimen has disappeared from the herbarium, and the identification is not certain." The following information has been received from Dr. Eric Hultén, Botaniska Museet, Lund, Sweden, "As far as I have been able to find there is no specimen of *Ranunculus Eisenii* in Swedish herbaria. I have never seen any Californian specimens collected by Eisen in Swedish Museums." We adopt the interpretation of Dr. Gray, Proc. Am. Acad. **21**: 373. 1886. His reference is to a plant identified by Torrey as *R. canus* Benth.; cf. Torr. Pac. R. R. Rep. **4**: 62. 1857. The collection was cited as follows: "Hill sides, Duffield's Ranch, Sierra Nevada; May 11." The specimen in the Gray Herbarium was collected by Bigelow.

5C. Ranunculus occidentalis Nutt. var. ultramontanus Greene, Pittonia **3**: 13. 1896. *R. alceus* Greene, Erythea **3**: 69. 1895. *R. ultramontanus* Heller, Muhlenbergia **6**: 11. 1910. *R. occidentalis* var. *alceus* Jepson, Fl. Calif. **1**: 540. 1922.

Meadows and along mountain streams at 1,300–2,000 meters elevation in the North Coast Ranges of California from Elk Mountain, Lake County, northward, and at 1,800–2,300 meters largely on the eastern side of the Sierra Nevada from Mt. Shasta to Inyo County and to near Reno and Carson City, Nevada; continuing northward in modified form and occurring at a few stations east of the Cascade Mountains in Southern and Central Oregon. Yellow pine forest. June and July. Cf. L. Benson in Abrams Ill. Fl. Pacif. St. **2**: 1940.

Type collections: (1) *R. alceus*, "Collected at an altitude of about 4,000 feet on Elk Mountain, Mendocino [Lake] Co., Calif., July, 1892, by Mr. Jepson." Elk Mountain is in Lake County. This error was corrected by Jepson, Fl. Calif. **1**: 540. 1922, "type loc. Elk Mt., Lake Co., Jepson." The type has not been located in the Herbarium Greeneanum or in Dr. Jepson's working collection. (2) Var. *ultramontanus*, "Banks of streams and lakes, or in moist meadows along the Truckee River, at the eastern base of the Sierra Nevada, Calif." The Herbarium Greeneanum has only one specimen collected by Dr. Greene prior to 1896, and it is chosen as a lectotype. It was obtained near Boca on the Truckee River, California, on July 24, 1895 (HGr 2726).

5d. Ranunculus occidentalis Nutt. var. dissectus Henderson, Rhodora **32**: 25. 1930. *R. ciliosus* Howell, Fl. N. W. Amer. **1**: 17. 1897. *R. marmorarius* Jepson & Tracy in Jepson, Fl. Calif. **1**: 542. 1922.

Meadows of mountains and high plains at 1,300–2,200 meters elevation; Eastern Oregon and the Rogue River-Umpqua River Divide; Marble Mountain, Siskiyou County, California. Yellow pine forest. June and July. Cf. L. Benson in Abrams, Ill. Fl. Pacif. St. **2**: 1940.

Type collections: (1) *R. ciliosus*, "Moist banks, in Bear Valley, Blue Mountains, Oregon. *Howell*, May 23, 1885." (2) *R. marmorarius*, "Marble Mt., western Siskiyou County [California], Chandler (type)." *Chandler 1891.* (3) Var. *dissectus*, "Dry slopes of Crater Lake Park, Oregon, near Pole Creek Bridge, where collected by *Lyle Wynd*, July 12, 1928. His no. 2221."

5E. Ranunculus occidentalis Nutt. var. Howellii Greene, Pittonia **3**: 14. 1896. *R. Howellii* Greene in Howell, Fl. N. W. Am. **1**: 17. 1897.

Openly wooded hills at 300–1,300 meters; Rogue River watershed in Jackson and Josephine Counties, southwestern Oregon. Northwestern coniferous forest and oak woodland. Late March to May or June. Cf. L. Benson in Abrams, Ill. Fl. Pacif. St. **2**: 1940.

Type collection: "Dry hillsides near Ashland, Oregon, 1899; collected by Mr. Howell." *Howell 1331.*

5F. RANUNCULUS OCCIDENTALIS Nutt. var. **montanensis** (Rydb.) L. Benson, comb. nov. *R. montanensis* Rydb. Mem. N. Y. Bot. Gard. **1**: 166. 1900.

Stems erect or decumbent at the bases, 3–6 dm. long and 3–7 mm. in diameter; radical leaves simple, semicircular in outline, 2–5 cm. long, 3–10 cm. broad, 3-divided or nearly so, the divisions again 3–5-lobed and proximally narrowly cuneate and distally acute, pilose with spreading or somewhat appressed hairs, the ultimate lobes acute, but not triangular, the sides curving; petals 5, rarely 10, 8–11 mm. long, 6–7 mm. broad, 1.2–1.5 times as long as broad; achenes 15–45 (the other varieties 8–20), achene body obovate, 2.5 mm. long, 2 mm. broad, glabrous, the beak about 1 mm. long, recurved, falcate, often bent rather sharply at the middle; receptacle globose, 2.5 mm. long in fruit (about 1.5 in the other varieties.)

Wet meadows, 1,500–2,500 meters elevation; Boise, Custer, and Blaine Counties and Beaver Canyon, Idaho; western Montana; western edge of Wyoming; Albuquerque, New Mexico (?). Yellow pine forest. June and July.

Closely related to *R. acriformis* A. Gray and to *R. occidentalis* var. *Nelsonii.*

Type collection: "MONTANA: Helena, 1891, *F. D. Kelsey* (type)."

5G. RANUNCULUS OCCIDENTALIS Nutt. var. **Nelsonii** (DC.) L. Benson, comb. nov. *R. recurvatus* Poir. var. *Nelsonii* DC. Syst. **1**: 290. 1818. *R. Nelsonii* A. Gray, Proc. Amer. Acad. **8**: 374. 1872. *R. repens* L. var. *major* Nakai, Bot. Mag. (Tokyo) **42**: 23. 1928. *R. Nelsonii* subsp. *insularis* Hult. Svensk. Bot. Tidskr. **30**: 526. 1936.

Stems erect, 4–7 dm. long, usually 2–6 mm. in diameter, branching above, the lowest internode usually 1.5–3 dm. long, strongly fistulous, hirsute; radical leaf blades simple, 2.5–4.5 cm. long, 2.5–7 cm. broad, deeply 3-parted and each primary part again 3–9-lobed or -toothed, proximally cordate and distally rounded or obtuse in outline; sepals 5 or in 1 specimen some flowers with 6; petals 5–6, 7–9 mm. long, the nectary scale glabrous, free laterally, the non-glandular portion 3–5 times as broad as long, truncate; each achene asymmetrically obovate, 3 mm. long, 2.5 mm. dorsiventrally, 0.5 mm. laterally, glabrous, the achene beak about 0.6 mm. broad at the base, 1.2–2 mm. long, recurved, commonly markedly falcate.

Moist ground at low elevations along the cost of Alaska and in the Aleutian Islands. Northwestern coniferous forest. June and July.

Type collections: (1) Var. *Nelsonii,* "In insulâ Unalasckâ unâ ex Aleutienis. D. Nelson." (2) Var. *major.* According to Hultén this variety is *R. Nelsonii.* According to information supplied by Dr. H. W. Rickett of the New York Botanical Garden, "Nakai's collections are from Corea. Other collections which he cites are from Sachalin, Kuriles, Yeso." (3) Subsp. *insularis.* The following is quoted from Hultén by Dr. Rickett; Aleutian Islands: Amchitka, July 9, 1932. Hn No. 6463 (type). ("Distributed to several European and American Museums.")

5H. RANUNCULUS OCCIDENTALIS Nutt. var. BREVISTYLIS Greene, Pittonia **3**: 14. 1896.

Practically glabrous; primary divisions of the radical leaf blades only 3–4-lobed or -toothed; sepals 5, reflexed; petals 5 usually narrowly obovate, emarginate or rounded, 7–10 mm. long, 5–6 mm. broad, the nectary scales only 1.5–2.5 times as broad as long, apically rounded; base of the achene beak 0.4–0.5 mm. broad; similar otherwise to var. *Nelsonii.*

Moist ground; Yes Bay and Loring, southern tip of Alaska. Northwestern coniferous forest. Summer.

Significant specimens: ALASKA: Yes Bay, *Howell 1602, HGr*, NY, S; Loring, Chamberlain 26 in 1903, NY.

5I. RANUNCULUS OCCIDENTALIS Nutt. var. **Turneri** (Greene) L. Benson, comb. nov. *R. Turneri* Greene, Pittonia **2**: 296. 1892.

Hirsute; primary divisions of the radical leaf blades 3-lobed, "the lateral lobes bifid, all incisely cleft;" sepals 5, spreading; petals 5, broadly obovate, truncate, 12–14 mm. long, the nectary scale unknown; achene beak long and slender, recurved.

Moist ground; Porcupine River, Northeastern Alaska. Northern coniferous forest. Summer.

Type collection: "We are glad to be able to dedicate so fine a new plant to the gentleman who has given the very best of recent contributions to our knowledge of Alaskan vegetation, Mr. J. H. Turner, who brings it from Porcupine River." TYPE, *Turner* in 1891, *HGr 2811.*

5J. RANUNCULUS OCCIDENTALIS Nutt. var. **hexasepalus** L. Benson, var. nov. Hirsute; primary divisions of the radical leaf blades 5–13-lobed or -toothed; sepals usually 6 (a number unique in *Ranunculus*) reflexed; petals 8–12, obovate or narrow, distinctly emarginate, 11–13 mm. long, 3–4 or 7–8 mm. broad, the nectary scale once or twice as broad as long, truncate or obtusely pointed; fruit unknown.

Hirsuta; partibus primariis folii 5–13 lobatis; sepalis plerumque 6, reflexis; petalis 8–12, obovatis, emarginatis, 11–13 mm. longis, 3–4 vel 7–8 mm. latis; squamulis nectarii latis.

Moist ground; Queen Charlotte Islands, British Columbia. Northwestern coniferous forest. Summer.

Type collection: Queen Charlotte Islands, *Rev. J. H. Keen 10* in 1898. TYPE in the New York Botanical Garden.

Significant specimens: BRITISH COLUMBIA: Queen Charlotte Islands, *Boas 86* in 1901, NY; Skidegate (?) Inlet, Queen Charlotte Islands, *Newcombe* in 1897 (*Geol. Surv. Can. 18054*), *HGr 2993.*

6. RANUNCULUS CALIFORNICUS Benth. Pl. Hartw. 295. 1848. *R. Deppei* Nutt. in Torr. & Gray, Fl. N. Amer. **1**: 21. 1838, as syn. *R. dissectus* Hook. & Arn. Bot. Beech. Voy. 316. 1840. Not Bieb. in 1819. *R. californicus* var. *latilobus* A. Gray, Proc. Am. Acad. **21**: 375. 1886. *R. latilobus* Parish, Pl. World **20**: 214. 1917.

Vernally moist land of north slopes, meadows, fields, and rolling hills; seaward coastal ranges from Humboldt County, California to Ensenada, Baja California; inland from San Francisco Bay to the Sierra Nevada at Volcano, Amador County and the foothills east of Madera. Oak woodland. Late January to May.

A form with the floral parts resembling vegetative leaves occurs in adobe soil in the San Francisco Bay Region. North Coast Range varieties of *R. occidentalis* and *R. canus* occasionally exhibit the same tendency. A five-petalled form occurs in San Diego County. (Laguna Mts., *Munz 9705*, *Sanford* in 1927; Julian, *M. E. Jones* in 1906, *J. D. Randall* in 1914; Santa Ysabel, *Henshaw 200*.) This form might be included in *R. occidentalis* var. *Eisenii* because of the presence of only 5 petals. However, the other characteristics seem to agree with those of the form of *R. californicus* growing in the San Jacinto Mountains and in the mountains of San Diego County. This form has unusually small fruit. In vegetative characters it agrees more fully with *R. canus* var. *Ludovicianus* than with *R. californicus.*

Type collections: (1) *R. Deppei*, "*R. acris* (Linn.) . . . β. hairy; petals oblong, 10–14.—R. Deppei *Nutt.! mss.* . . . California, *Nuttall!* June." (2) *R. dissectus*, "California-Supplement. Where not otherwise mentioned, it is to be understood that the following species are from the collection of Mr. Douglas. They were presented by the Horticultural Society of London, in whose service Mr. Douglas was at the time he gathered them." (3) *R. californicus*, *Hartweg* "1628 (155) . . . *R. dissectus*, Hook. et Arn. Bot. Beech. p. 316, non. Bieb.—In sylvis prope Monterey," collected in 1846–7. An isotype from Hartweg's collection (Gray Herbarium) is the same peculiar dissected-leaved form as the plant upon which *R. dissectus* was based (isotype also in the Gray Herbarium). No other collections of the species quite match these two isotypes! (4) Var. *latilobus*, "A common coarse-leaved and more robust form, *R. Ludovicianus* Greene, Bull. Calif. Acad. ii. 58." Greene, Fl. Fran. 300. 1892, wrote as follows: "Var. (4) *latilobus*, A. Gray, Proc. Am. Acad. xxi. 375 (1886), in part, excl. *R. Ludovicianus*. . . . Var. 4 is n. 374 of the State Survey from Santa Barbara." Gray's brief description throws no light on the subject, and he gave no indication that *Brewer 374*, Geological Survey of California, from Santa Barbara was the type of his variety. However, it is not likely that he had seen the type of *R. Ludovicianus*, since none of the original material of it is at the Gray Herbarium or apparently elsewhere. Furthermore, in the Synoptical Flora of North America (**1**: 35. 1895) the variety *latilobus* is said by Robinson to be "a common form, especially southward, from San Francisco Bay to San Diego and San Bernardino," while *R. Ludovicianus* (now transferred to *R. canus* as a variety) is confined to fairly high elevations of the Tehachapi and San Bernardino Mountains in the interior. The description in the Synoptical Flora is too general to be of value in determining the identity of the variety. However, the material at the Gray Herbarium labelled for the Synoptical Flora as var. *latilobus* is definitely typical *R. californicus*. Since the Synoptical Flora label is on *Brewer 374*, the writer accepts it as representative of the plants to which the name *latilobus* was given, because Robinson was in a better position than anyone else to know what Gray intended. It is to be noted that Parish (l.c. 1917) took up the name *latilobus* as a specific epithet intended for var. *Ludovicianus*. Otherwise, interpretations have been generally the same as Greene's and Robinson's.

6A. RANUNCULUS CALIFORNICUS Benth. var. GRATUS Jepson, Fl. W. Mid. Calif. 201. 1901.

Wet banks and bottom land of deep canyons or moist north slopes; Curry County, Oregon to Napa County and the Monterey Peninsula in California.

Northwestern coniferous forest (inner edge of the redwood belt). Late February to May. Cf. L. Benson in Abrams, Ill. Fl. Pacif. St. **2**: 1940.

This variety appears to pass into *Ranunculus occidentalis* var. *Eisenii* in Mendocino, Sonoma, and Napa Counties and into *Ranunculus californicus* from Sonoma County southward. It is best-developed in Sonoma and Santa Clara Counties, and the extreme form is strikingly differentiated from *Ranunculus californicus*. Segregation of the variety in Mendocino County and northward is difficult.

Type collection: "Commonly in wooded country: hills of Napa Valley; Vaca Mountains."

6B. RANUNCULUS CALIFORNICUS Benth. var. CUNEATUS Greene, Fl. Fran. 299. 1892. *R. californicus* var. *crassifolius* Greene, Erythea **1**: 125. 1893.

Barren sea bluffs; Sauvies Island, Columbia River, Oregon to Monterey County, California; Santa Maria, San Miguel, and Santa Cruz Islands. Northwestern coniferous forest region. May and June. Cf. L. Benson in Abrams, Ill. Fl. Pacif. St. **2**: 1940.

Oregon specimens tend toward 5 petals and compound leaves. They are as closely related to *R. occidentalis* as to *R. californicus*.

Type collections: (1) Var. *cuneatus*. "Var. 3 is confined to the wet meadows that lie back of the ocean in San Mateo Co., doubtlessly also reaching San Francisco Co. In cultivation at Berkeley it behaves very unlike the other forms, is almost annual, i.e. many individuals come to flowering the first year from seed, and die before the end of the year. Other individuals are of perennial duration." No type was found by the writer at the Herbarium Greeneanum, Notre Dame University. Specimens cultivated at Berkeley by Dr. Greene in 1893 and 1894 are at the Herbarium of the University of California. These were pressed one and two years after publication of the variety. However, they represent perhaps the stock from which the variety *cuneatus* was described, and they are the nearest approach to a type. (2) Var. *crassifolius*, "Collected at Fort Bragg, Mendocino Co., Calif., by Mr. Michener." The type of this variety also failed to be located at the Herbarium Greeneanum, and the writer has seen no isotype.

6C. RANUCULUS CALIFORNICUS Benth. var. RUGULOSUS (Greene) L. Benson, Am. Jour. Bot. **23**: 30. 1936. *R. rugulosus* Greene, Pittonia **2**: 58. 1890.

Wet sand of rivers and ditches up to 1,000 meters elevation; California; tule land along the Sacramento River in Sutter County; San Joaquin Valley from western Merced County to Kings and Tulare Counties; lower Sierra Nevada foothills from Tuolumne County to Mariposa County. March to May. Cf. L. Benson in Abrams, Ill. Fl. Pacif. St. **2**: 1940.

Type collection: "The type of this species is a very slender but tall plant from the Chowchilla Mountains in the eastern part of south-central California, where it was collected in 1875 by Mr. F. P. McLean." The "Chowchilla Mountains" are a ridge in the Sierra Nevada west of Wawona, Yosemite National Park. The TYPE is HGr 2799.

7. RANUNCULUS CANUS Benth. Pl. Hartw. 294. 1848. *R. occidentalis* Nutt. var. *canus* A. Gray, Proc. Am. Acad. **8**: 374. 1872. *R. californicus* Benth. var. *canus* Brew. & Wats. Bot. Calif. **1**: 8. 1876. *R. canus* var. *Blankinshipii*

Rob. in A. Gray, Syn. Fl. N. Am. **1**: 35. 1895. *R. Blankinshipii* Heller, Muhlenbergia **1**: 40. 1904. *R. longilobus* Heller, Muhlenbergia **2**: 36. 1905.

Heavy soils of hills and valleys at 20–300 meters elevation; California; inner Coast Ranges from Tehema County to the Mt. Diablo Range; Sacramento Valley; lower Sierra Nevada foothills (below the oak belt) from Butte County to Tuolumne County; San Joaquin Valley in San Joaquin County and at Merced and Lindsey. Late February to early April. Cf. L. Benson in Abrams, Ill. Fl. Pacif. St. **2**: 1940.

The name *Ranunculus canus* is taken for the plants of the *R. occidentalis* complex having fruit 4–5 mm. long. In the Coast Range and the Sierra Nevada foothills it is not unusual to find on the same plant the large fruit of *R. canus* and the (usually) relatively small, simple leaves of *R. occidentalis* var. *Eisenii*, which grows in both ranges at higher elevations or at stations more remote from the Sacramento Valley than does *R. canus*. This form has been named *R. canus* var. *Blankinshipii*.

Type collections: (1) *R. canus*, "In pascuis humidis vallis Sacramento ubi terram late obtegit." *Hartweg 1626* (*239*) in 1847. Jepson, Erythea **5**: 54. 1897, quotes the following from Hartweg: "On April 13, I left [the junction of the Yuba and Feather Rivers] with Mr. L. for his farm seventy miles higher up the valley. . . . Crossing Feather River, which here is eighty yards broad, and of considerable depth, our course lay five and twenty miles along that river, through a beautiful wood of evergreen and deciduous oaks. . . . Leaving Feather River we struck across a prairie for twenty miles; here immense fields of *Eschscholtzia crocea*, *E. californica* and *Ranunculus No. 239*, presented themselves, each species growing by itself." The junction of the Yuba and Feather Rivers is at the present town of Marysville; Oroville is 26 miles up the Feather River; Chico is 21 miles northwest of Oroville. The country between Oroville and Chico is treeless grassland. The type station for *R. canus*, therefore, must be between Oroville and Chico. A few collectors have obtained the species on the plains and foothills between the towns in recent years. (2) Var. *Blankinshipii*, "Capay, Yolo County, Calif., J. W. Blankinship. 15 April, 1893." (3) *R. longilobus*, "The TYPE is [*Heller*] no. 7912, collected May 31, 1905 on hills about one mile back from Middle Creek Station near Keswick, Shasta county, California, growing in damp ground near a little stream." This plant is intermediate in vegetative characters between *R. occidentalis* vars. *Eisenii* and *ultramontanus*, and both the type collection and a specially-collected topotype (*Heller 13930*) show fruit partly of the *R. canus* type and partly of the *R. occidentalis* var. *Eisenii* type. While *R. longilobus* is placed in synonymy under *R. canus*, the type is by no means identical with that species. The Middle Creek Station plants seem to represent a local population derived by recombination of characters of *R. canus* and *R. occidentalis* vars. *Eisenii* and *ultramontanus*. It is doubtful if the population is sufficiently homogeneous and consistently differentiated to be considered as a separate variety. However, this point might be determined by intensive field work at and near the type locality. Herbarium specimens are inadequate for such a study.

7A. RANUNCULUS CANUS Benth. var. LAETUS (Greene) L. Benson in Abrams, Ill. Fl. Pacif. St. **2**: 1940. *R. californicus* Benth. var. *laetus* Greene, Fl. Fran. 299. 1892. *R. californicus* var. *canescens* Greene, Fl. Fran. 299. 1892. *R. hesperoxys* Greene, Erythea **2**: 189. 1894. *R. canus* var. *hesperoxys* Davis, Minn. Bot. Stud. **2**: 475. 1900.

Heavy adobe soil on north slopes of foothills; California; Marysville Buttes; Woodland; Vaca Mountains; Mt. Diablo Range; San Joaquin Valley near Stockton. March and early April. Cf. L. Benson in Abrams, Ill. Fl. Pacif. St. **2**: 1940.

Intermediates between the variety and *R. canus* occur in the Sacramento Valley. West and south of the Mt. Diablo Range, the leaf form of var. *laetus* is found combined with the characteristics (small fruit and 9–16 narrower petals) of *R. californicus*.

Type collections: (1) Var. *laetus*, "Var. 1 is of the interior, about Suisun . . . occupying low meadow lands adjacent to brackish marshes." Greene's specimen collected at Suisun on May 4, 1890 is designated as a LECTOTYPE (HGr 2542). (2) Var. *canescens*, "Var. 2 belongs to middle elevations of the Mt. Diablo Range and the valleys among them, from Niles to the hills east of Livermore, thence southward to San Luis Obispo County. It was in part my *R. Ludovicianus.*" The following specimens are at the Herbarium Greeneanum: near Livermore, *Greene*, March 9, 1889 (HGr 2528–9); Paso Robles, *C. C. Parry* in 1888 (HGr 2527). Since there is no material from Niles, the first-mentioned locality, the Livermore specimen is designated as a lectotype. The Parry specimen is densely hairy like var. *laetus*, but the fruit and flower characters place it in *R. californicus*. (3) *R. hesperoxys*, "This is the plant, which in the *Flora Franciscana* and in the *Manual*, I called *R. canus*, for the reason that it seemed to come nearer the description of that species than any other plant known to occur in the region whence Mr. Bentham had his type. But having now seen that type, I am prepared to assert that *R. canus* had not yet been rediscovered. Nothing at all resembling Hartweg's plant is known to Californian botanists of the present time." In *Flora Franciscana* (301. 1892) *R. canus* is said to occur on "Plains and hills of the interior, especially about Antioch, and northward to Chico, *Mrs. Bidwell.*" The following specimen is designated as a LECTOTYPE: Antioch, *Greene*, April 6, 1887 (HGr 2615).

Representative specimens: CALIFORNIA: Marysville Buttes, *L. Benson 6352*, B; Woodland, *Blankinship* in 1893, GH; Gordon Valley, Napa County, *Greene* in 1886, *HGr;* Suisun, *Greene* in 1885, *HGr*, UC., in 1895, *HGr*, UC.; Antioch, *Greene* in 1887, *HGr*, UC, in 1895, *HGr*, UC. Davy 915, *HGr;* Mt. Diablo, *Greene* in 1886, *HGr;* Livermore, *Greene* in 1889, *HGr;* Knight's Ferry, *Bancroft* in 1895, J, *HGr;* San Joaquin County, *Stanford*, S.

7B. RANUNCULUS CANUS Benth. var. LUDOVICIANUS (Greene) L. Benson in Abrams, Ill. Fl. Pacif. St. **2**: 1940. *R. ludovicianus* Greene, Bull. Calif. Acad. **2**: 58. 1886. *R. californicus* var. *ludovicianus* Davis, Minn. Bot. Studies **2**: 476. 1900.

Moist ground of vernal meadows or rivulets or mountain streams at 1,000–2,300 meters elevation; Temblor, Greenhorn, Tehachapi, San Gabriel, and San Bernardino Mountains of South-Central and Southern California. Yellow pine forest and oak woodland. Late March to May. Cf. L. Benson in Abrams Ill. Fl. Pacif. St. **2**: 1940.

Type collections: (1) *R. ludovicianus*, "High valleys among the mountains of San Luis Obispo County, California, and eastward to Tehachapi Pass. Collected by Mrs. Curran, in 1884." Neither the Brandegee Collection at the University of California nor the Herbarium Greeneanum contains a specimen collected by Mrs. Curran (Brandegee) in San Luis Obispo County, and no specimen of this variety has been collected in San Luis Obispo County at any other time. The epithet *ludovicianus* has been consistently applied to the common many-petalled plant growing in the Tehachapi Mountains, and the writer believes that, in absence of a type, established custom should be law. The 1884 collection from Tehachapi by Mrs. Curran (Brandegee) is designated as a LECTOTYPE, and, in the event that it is not rediscovered, the 1895 collection by Mrs. Brandegee (Herbarium of the University of California) should be considered a substitute for it. The 1884 specimen is to be found in neither the University of California Herbarium nor the Herbarium Greeneanum. *Ranunculus californicus* var. *latilobus* is an epithet attributed by some botanists to this plant (cf. discussion under *R. californicus*).

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VARIABILITY IN WOOD STRUCTURE IN ROOTS OF NATIVE ONTARIO CONIFERS

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(WITH EIGHTEEN FIGURES)

INTRODUCTION

The present paper is one of a series on the wood structure of conifers. Its scope is limited to consideration of variability in the secondary xylem of roots of such native species as *Thuja occidentalis*, *Tsuga canadensis*, *Abies balsamea*, *Larix laricina*, *Picea glauca*, *P. mariana*, *Pinus Banksiana*, and *P. Strobus*. Material was collected from trees in different types of habitat and from different parts of the root systems, so that some conception might be obtained of the range of variation within the individual, the differences between trees in varied habitats, and the relationships, if any, between wood structure and environment. The bearing of the variability in structure upon the identification of coniferous woods, both living and fossil, is discussed.

The root systems of the native conifers differ. *Larix laricina* and *Picea mariana* under most conditions, and *Thuja occidentalis* and *Picea glauca* when growing in swamps, have shallow root systems made up largely of widely spreading horizontal roots confined to the top few inches of soil. In dry soils, especially sand, *Thuja*, *Picea glauca*, and *Pinus* spp. generally have sinker roots in addition to the laterals. These deep roots include the tap root, when present, and other roots which extend downward from the principal horizontal roots. In the following descriptions these deep roots are designated as vertical roots, and the horizontal roots located close to the surface as lateral roots.

GROWTH RINGS AND SIZE OF TRACHEIDS

The width of the growth rings was found to be highly variable. Of adjacent rings one sometimes was wide while those preceding or succeeding were narrow. Some rings were more or less uniform in width around the circumference, others were decidedly eccentric. The greatest eccentricity was observed in certain lateral roots near the stem, and in vertical roots wedged between stones. On the other hand, many lateral roots, and most vertical roots growing in sand, were more or less round.

Generally the growth rings were wider in roots growing in wet soils than in dry sand. In material of *Thuja*, *Tsuga*, *Larix*, and *Picea mariana* the average differences in ring width between roots from wet and dry sites ranged from 25 to 50 per cent.

The proportion of early and late wood in the growth rings, the size of the tracheids, and the thickness of their walls, varied greatly in different parts of the root system and in different specimens. The study of large numbers of roots revealed some correlation between character of the wood and location in the root system, and sometimes with the depth in the soil, but it should be emphasized that the wood structure was exceedingly variable, even in different parts of the same root.

Usually, the largest tracheids and the least development of late wood were observed in the inner wood, to a distance of 1 cm. or more from the primary xylem, in the distal parts of lateral roots of mature trees. This type of wood was best developed in these lateral roots located in the upper few inches of soil, but at no point exposed, and several feet distant from the bole (fig. 3).

A more stem-like wood in which the tracheids were smaller in diameter, the walls thicker, and late wood more extensive (figs. 1, 2), was found in the following kinds of roots or in roots growing under the following conditions: (1) the wood in the proximal portions of the roots of small trees two or three feet high; (2) the wood on the upper side of large buttress roots belonging to mature trees; (3) the outer wood, around the whole circumference, of some of the larger lateral roots, both close to and as far as ten feet or more from the stem; (4) the wood formed on the upper side of lateral roots after they have been uncovered by soil erosion, irrespective of size of the root or distance from the stem; (5) some of the more or less superficial lateral roots of adult trees growing in meadows or swamps which tended to become dry during the summer; (6) certain of the vertical roots extending down into the ground.

The above descriptions hold generally for the conifers listed in the introduction, but there was evidence that the range of variation in various parts of the root system and in roots growing under varied environmental conditions was greater in some species than in others. For instance, the average differences in size between the tracheids of lateral and vertical roots were much greater in *Picea* spp. than in *Thuja occidentalis* (table 1).

The nature of the factors involved in the development of the stem-like type of wood in some roots was not clear, although certain circumstances were noted which evidently played some part. For instance exposure of certain roots resulted in a change in wood structure. An example in which

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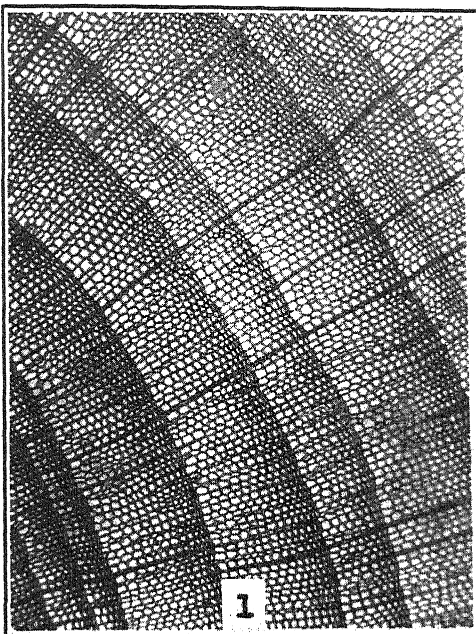
Explanations of figures 1–5.

FIG. 1. *Picea glauca.* Stem-like wood in vertical root, 3 feet deep in uniform sand. × 40. FIG. 2. *Picea mariana.* Stem-like wood in vertical root wedged between stones. × 40 FIG. 3. *Picea glauca.* Open type of wood in lateral root 24 feet from the stem, approximately 2 inches deep in sand. × 40. FIG. 4. *Picea mariana.* Abnormal tissue in lateral root. × 150. FIG. 5. *Picea mariana.* Alternate and opposite arrangements of pits in the radial walls of tracheids in lateral root. × 330.



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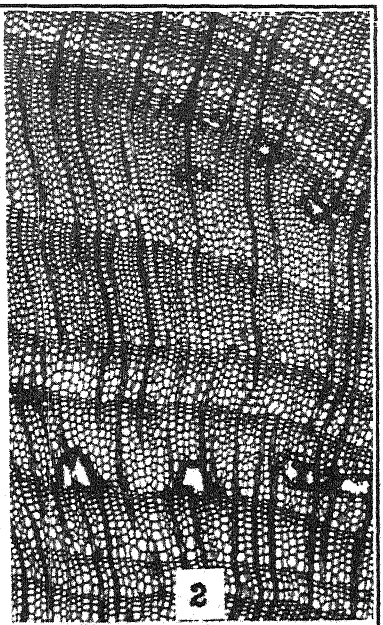

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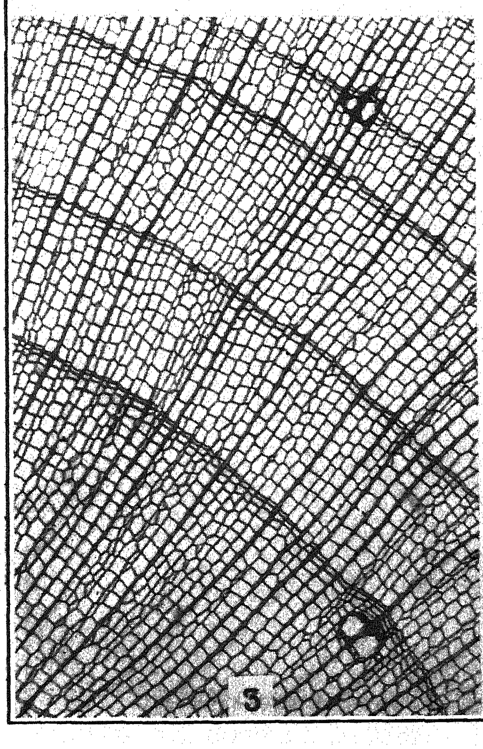

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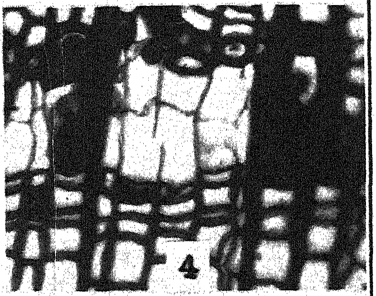

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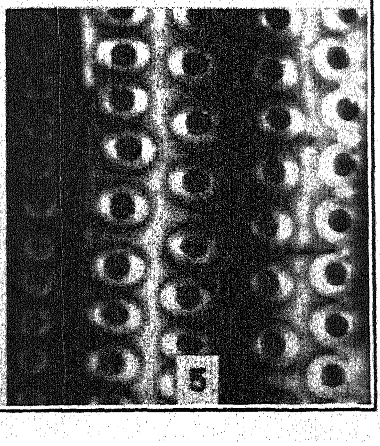

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TABLE 1

Average radial and tangential dimensions of early-wood tracheids in root wood at distances of 1 to 3 mm. from the primary xylem

Species	Lateral roots	Vertical roots
Thuja occidentalis (67 roots)	42 × 27 μ	40 × 25 μ
Picea mariana (53 roots)	48 × 29 μ	36 × 23 μ
Picea glauca (42 roots)	46 × 28 μ	34 × 22 μ

such a relationship was indicated has been described and illustrated in a previous article (Bannan 1937) for *Thuja occidentalis*. Similar correlation was observed in exposed lateral roots of other genera.

On the other hand, some circumstance other than exposure was evidently operating to produce the stem-like wood found in some roots well below the surface of the ground. Certain vertical and oblique lateral roots of *Picea*, located at depths of 1–2 feet in gravelly and stony soils, exhibited a transition from a more or less open type of wood near the center to a fine-textured stem-like wood in the outer rings. Vertical roots of such western species as *Pinus ponderosa*, *Tsuga heterophylla*, and *Libocedrus decurrens* excavated from gravel were also found to resemble in this respect the roots of *Picea* described above. In most roots the change in wood type took place while they were still quite small, not more than 1 or 2 cm. in diameter.

In other vertical roots of *Picea* (*P. glauca*) the wood was stem-like from the center. Such a uniform stem-like wood was observed in roots growing at depths of 2–4 feet in medium or coarse sand without gravel or stones. On the other hand, vertical roots of *Tsuga canadensis* at similar depths in fine sand were less stem-like. In these roots the wood varied considerably from one specimen to another, and even in different parts of one growth ring at the same level in the root. Considerable variation was also found in vertical roots of *Thuja occidentalis* at like depths in fine sand. Some of the roots exhibited a transition from an open wood near the center to a rather stem-like wood in the outer rings, but in others the wood was more or less uniformly intermediate in character. The factors responsible for these differences were not determined.

The age of the tree appeared to have some influence upon the wood structure. The wood in the proximal parts of the roots of small trees up to 2 or 3 feet in height was usually stem-like. The youth of the trees suggests that here some ontogenetic factor was involved.

Another circumstance having some effect on the wood structure, particularly in the lateral roots of mature trees, was distance from the stem. In most of the forms studied late wood was less extensively developed and the tracheids became larger in diameter at increasing distances from the bole. The extent of this tracheid enlargement is illustrated in figure 13 for *Larix* and *Picea*. In *Thuja*, on the other hand, there was little difference. No measurements were made of the tracheids in roots of *Tsuga canadensis*, *Pinus Banksiana*, or *P. Strobus*, but the trend appeared to be similar to that illustrated for *Larix* and *Picea*.

No consistent relationship was discovered between the size of the tracheids in lateral roots and the amount of soil moisture. Measurements were made of some 70 roots of *Larix laricina*, collected from four sites, two wet and two dry. The radial and tangential dimensions of the early-wood tracheids in the inner wood, at distances from 6 to 19 feet from the stem, were as follows: 64 × 34 μ in roots growing in a swamp in southern Ontario; 60 × 32 μ in roots on elevated ground nearby, the soil a mixture of silt and sand; 71 × 37 μ in roots growing in water-soaked muck at the bottom of a creek flowing through a larch, black-spruce swamp in northern Ontario; 63 × 36 μ in roots on a neighboring sand plain where no water was encountered in excavations as much as 4.5 feet deep, the soil a medium or coarse sand.

In both comparisons between wet and dry sites the tracheids were slightly larger in the roots growing in swamps. However, a trend in the opposite direction was observed in the roots of *Picea mariana*. Here the tracheid dimensions in lateral roots obtained from three sites were: 43 × 27 μ in swampy silt-sand soil in southern Ontario; 46 × 29 μ in dry medium or coarse sandy soil, northern Ontario; 54 × 29 μ in dry gravelly soil, northern Ontario.

In *Thuja occidentalis* very little difference was discovered between roots in wet and dry soils. Roots were collected from a number of sites in southern Ontario, and the average measurements were 42 × 29 μ in dry soils (sandy hilltops), and 42 × 26 μ in cedar swamps. All the values represent the outside dimensions of the tracheids, that is the distances between the middle lamellae. The measurements were based upon the early-wood tracheids in the inner wood, 1–3 mm. from the primary xylem, in lateral roots at points 6–19 feet distant from the stem.

The observations recorded fail to indicate the existence of any consistent relationship between tracheid size and soil moisture. Diverse tendencies appeared in the species studied, and much dissimilarity was found between trees of the same species growing under like soil conditions, and sometimes between roots of the same tree.

A search of the literature revealed that some work has been done on the texture of wood in stems, but apparently none on roots. Harlow (1927), reporting on tracheid diameters in stem wood of *Thuja occidentalis*, found greater variation between trees on the same site than between the averages of two extreme sites, though the trees on limestone soil had slightly smaller tracheids than trees on a peat bog. Myer (1930) found the intra-regional variation to be much greater than the inter-regional variation. The average tangential diameter of tracheids in the stem of *Tsuga canadensis* growing on a spruce flat was 4.4 per cent greater than in trees on a slope, but on the latter a 17 per cent variation was observed. According to Kienholz (1931) tracheids in the wood of *Pinus contorta* were larger in trees in sphagnum bogs than on other sites.

TRACHEID PITTING

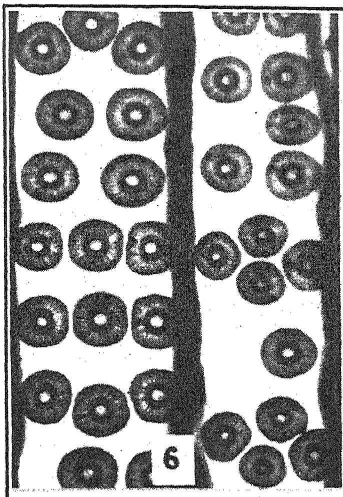
The bordered pits in the radial walls of tracheids in the secondary xylem of the native conifers are usually opposite, but as Thomson (1913) has shown in *Larix*, and Bailey (1933) has indicated for most of the other genera, an alternate arrangement is not uncommon. The latter is frequently to be seen in the first 20–30 growth rings in the distal parts of lateral roots of *Abies, Tsuga, Larix, Picea,* and less often in *Thuja* and *Pinus*. The more common opposite arrangement with conspicuous crassulae (rims of Sanio) is illustrated in figure 7, and without crassulae in figure 8. An alternating arrangement is shown in figures 8 and 9. Very wide tracheids often have three rows of pits, which may be grouped, opposite, or alternate, and crassulae may be present or absent (fig. 6). A similarly wide range of variation in arrangement of pitting and development of crassulae was observed in *Abies, Larix,* and *Picea* (figs. 10–12).

The alternating arrangement of pits occurred most frequently toward the overlapping ends of the tracheids where the pits were aggregated. It was found most often in the inner wood of lateral roots, seldom in the outer wood or in vertical roots. No outstanding generic distinctions in the proportion of alternate and opposite pits were noted between *Abies, Tsuga, Picea,* or *Larix,* but in *Thuja* and *Pinus* alternating arrangements were less numerous.

Some differences were observed in the torus and pit membrane. In *Abies* and *Tsuga* heavy bands extended across the membrane, usually in a radial direction from the rim to the torus (figs. 7, 8), but occasionally in a more or less tangential direction so as merely to come in contact with one side of the torus (fig. 9) or to avoid it completely. These bands gave the same staining reactions with ruthenium red and haematoxylin as the torus. They were not present in all pits, but generally were quite conspicuous in these two genera. They were seldom observed in *Larix, Picea* or *Pinus*. In the latter genera the margin of the torus is finely serrate (figs. 5, 10).

Explanation of figures 6–12.

Arrangements of pits on the radial walls of early-wood tracheids in the inner wood of the distal portions of lateral roots. FIG. 6. *Tsuga canadensis.* Grouped and opposite pits without crassulae. × 330. FIG. 7. *Tsuga canadensis.* Opposite pits with crassulae. × 330. FIG. 8. *Tsuga canadensis.* Alternate and opposite pits without crassulae. × 330. FIG. 9. *Tsuga canadensis.* Alternate pits, showing structure of the pit membrane. × 1300. FIG. 10. *Larix laricina.* Alternate pits. × 330. FIG. 11. *Larix laricina.* Alternate pits. × 330. FIG. 12. *Larix laricina.* Triseriate and alternate pits. × 330.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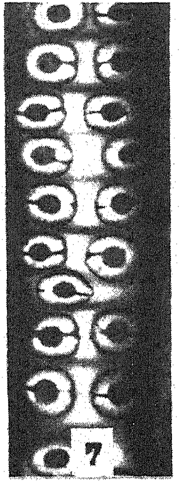
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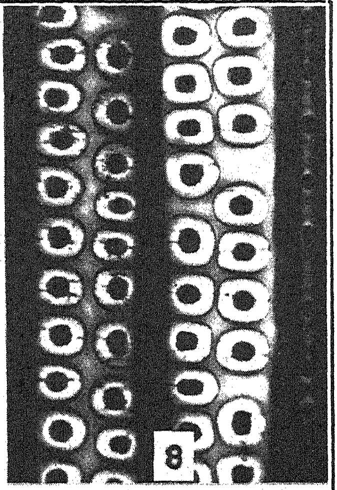
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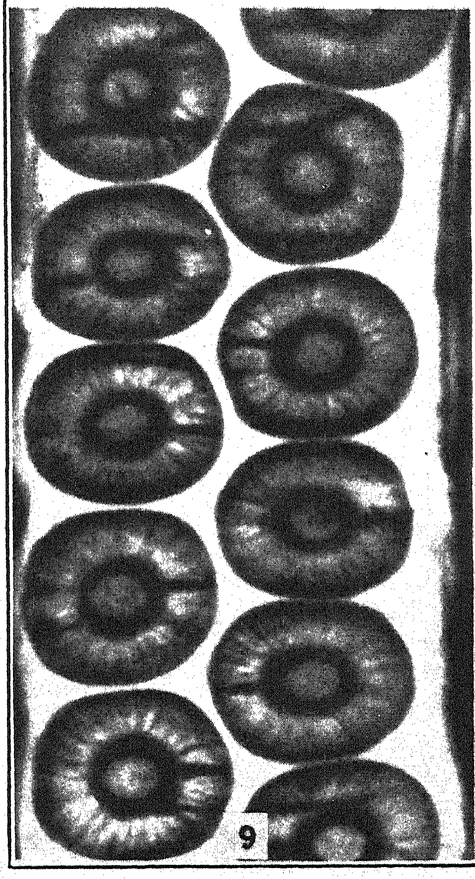
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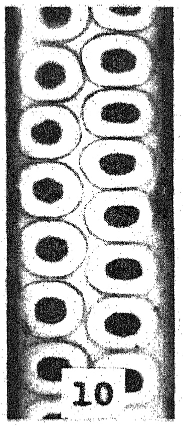
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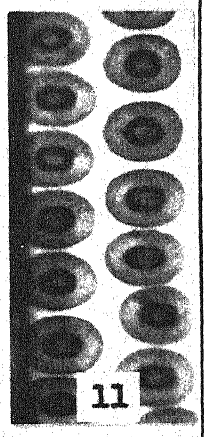
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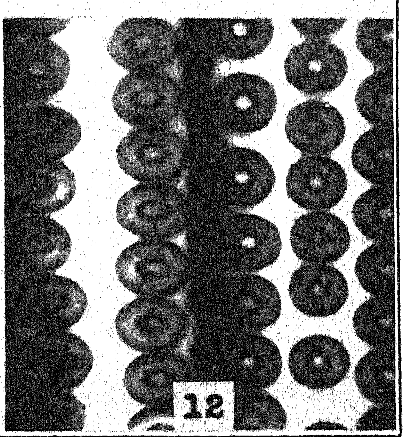
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VERTICAL PARENCHYMA

Vertical parenchyma, apart from that associated with resin ducts, is common in the roots of *Tsuga*, usually abundant but sometimes infrequent in *Larix*, and generally scarce but occasionally abundant in *Picea*. The cells are terminal in distribution. A few parenchyma cells were observed in a root of *Pinus Banksiana*, but since they were seen in a transverse section cut from material which in the meantime had been discarded, there was no way of ascertaining whether they were separate xylem parenchyma cells or were simply the enclosing cells of a resin duct which had ceased a short distance above or below. In the Abietineae studied no definite trends in distribution were noted in different types of roots, or in roots from varied habitats, nor were any peculiarities in structure observed which might serve to distinguish such similar woods as *Picea* and *Larix*. In *Thuja* vertical parenchyma is common though variable in distribution. The cells are usually scattered throughout the growth rings, but sometimes, particularly when clearly associated with injuries, occur in tangential arrangement.

That xylem parenchyma is erratic also in stem wood, especially in the Abietineae, has been shown by Bailey (1909). The distribution and frequency of xylem parenchyma have been used for distinguishing fossil woods, but studies of living conifers show this character to be too variable to have any diagnostic value.

Unlike the separate xylem parenchyma, the parenchyma cells surrounding the resin ducts in the Abietineae vary both with the genus and the part of the tree. For instance, the epithelium lining the ducts in the wood of *Larix* and *Picea* is made up partly of thick- and partly of thin-walled cells, but there are usually more thin-walled cells in *Picea* than in *Larix*, and in both genera the proportion of thin-walled cells is higher in roots and in the outer wood of old stems than in the inner stem or branch wood (Bannan 1936). It may be noted here that the proportions of thin-walled cells, as given for roots in the paper cited, applied only to lateral roots. In vertical roots the percentage of thin-walled cells is somewhat lower than in lateral roots, but higher than in branch or stem wood of similar size and age.

The nature of the epithelium of resin ducts is of some diagnostic value when utilized in conjunction with other characters. However, in view of the variation between individuals and different parts of the tree, the epithelium alone should not be regarded as an infallible character for separating woods which closely resemble one another in other features, as for instance *Larix* and *Picea*.

THE DISTRIBUTION OF RESIN DUCTS

The total number of vertical resin ducts in the first 15 growth rings in 154 lateral roots of *Picea* (*P. glauca* and *P. mariana*) and *Larix* (*L. lari-*

cina) collected from various sites ranged from 15 to more than 200. Roots of the larch were obtained from two places near Toronto, and two sites on the north shore of Lake Superior. Very great differences in the average number of resin ducts were discovered in the roots from these sites (table 2). The fewest ducts were found in roots dug from muck in the bottom of a creek flowing through a black spruce and larch swamp in northern Ontario, and the greatest number in roots growing in a rather open swamp adjoining a field in southern Ontario. The abundance of ducts in the southern Ontario material may have been due to injury by grazing animals, for most of the land has been pastured at one time or another, and the lateral roots, located close to the surface, are liable to be injured. In black spruce also more ducts were found in the southern Ontario roots. A noteworthy feature of the northern Ontario material was that more vertical ducts occurred in the roots growing in gravel than in roots in uniform sand (table 2).

TABLE 2

Number of resin ducts in lateral roots

Species	Habitat	Av. ring width (mm.)	Av. total no. of vertical ducts in first 15 growth rings	Av. no. of horiz. ducts per sq. cm. at 3–5 mm. from pr. xylem
Larix laricina	Elevated silt-sand soil, S. Ont.	0.25	89	46
	Low ground, open swamp, S. Ont.	0.37	124	42
	Medium to coarse sand, dry sand plain, N. Ont.	0.35	66	31
	Muck, creek in swamp, N. Ont.	0.36	38	33
Picea mariana	Low ground, open swamp, S. Ont.	0.35	112	122
	Dry gravelly and stony soil, N. Ont.	0.24	93	83
	Medium to coarse sand, dry sand plain, N. Ont.	0.25	53	85
Picea glauca	Medium to coarse sand, dry sand plain, N. Ont.	0.40	76	84

The distribution of ducts in vertical roots was even more variable than in lateral roots. The most numerous ducts were observed in vertical roots (and in some oblique lateral roots) of *Picea mariana* extending down into gravelly and stony soils. These roots were decidedly eccentric and much distorted, and transverse sections revealed areas of cell disarrangement and open injury, especially in the outer growth rings. Apparently these injuries were due to pressure exerted by the stones upon the enlarging roots wedged between them. Associated with the injuries were both extensive tangential series and scattered ducts (fig. 2).

Other vertical roots, particularly some of *Picea glauca* excavated from a medium to coarse sand without stones or other obstacles, had few ducts. The number in these was, on the average, only about half that observed in lateral roots growing on the same site, but closer to the surface of the ground. In fact, four of the vertical roots were almost lacking in ducts, the average total number in the first 15 rings being only 5, or an average of one duct every three rings. As is illustrated in figure 1, ducts were absent from large areas of the wood. The paucity of ducts was not attributable to lack of growth, since the rings were as wide as in roots with many ducts, but was evidently correlated with an absence of injury due to the nature of the medium in which the roots were growing.

The distribution of the horizontal ducts likewise varied greatly in different specimens. The horizontal ducts were more numerous in roots of both *Picea* and *Larix* collected in southern Ontario than in northern parts of the province, the distribution paralleling that of the vertical resin ducts in that respect (table 2).

The grand average number of horizontal ducts per sq. cm. of tangential section, determined at distances from 3 to 5 mm. from the primary xylem, was 84 in lateral roots of *Picea glauca*, 87 in *Picea mariana*, and 38 in *Larix laricina*. Similar numbers of horizontal ducts were observed in the outer rings, from 3 to 5 cm. from the center, in *Picea*, but in *Larix* the number in the outer rings was greater than in the wood nearer the center. Consequently the differences between the two genera observed in the inner wood tended to disappear in the outer rings. But even in the inner wood, where substantial differences were noted in the average values, the distribution was much too irregular to have any diagnostic value.

The roots of both larch and spruce are diarch as a rule, and in roots up to 1 cm. in diameter 20 per cent more horizontal ducts, on the average, were found in the radii parallel to the primary xylem plate than in the other sectors of the wood. Factors responsible for this increase were the origin of horizontal ducts from the primary, vertical ducts, and the greater numbers of rays in those radii.

The distribution of horizontal ducts in vertical roots (*Picea* spp.) was very erratic. They were numerous in some roots, particularly in those growing in gravel, and were scarce in others. In fact, in one root growing in a uniform sand the horizontal ducts were so rare as to be absent from tangential sections of considerable area. Vertical ducts also were very scarce in this root.

Since certain generic differences exist, the distribution of resin ducts has been used as a character for differentiating the secondary xylems of living Abietineae and of fossils of Abietinean affinity. In *Abies*, *Tsuga*, and *Pseudolarix*, ducts, when present, are always of the vertical type and are arranged in tangential rows. Similar tangential series occur in *Cedrus*, but in this genus there are also horizontal ducts. In *Keteleeria* only vertically oriented ducts have been reported. These appear to be confined to tangential series in some specimens, and are distributed throughout the wood in others. Both vertical and horizontal ducts are found in *Picea*, *Larix*, and *Pseudotsuga*. The vertical ducts are usually scattered, but in some cases tangential series are also formed, and on rare occasions all the ducts are tangentially arranged. *Pinus*, likewise, has both vertical and horizontal ducts, but the former are generally dispersed throughout the wood and extensive tangential series very seldom occur in living species. The usual practice in the literature has been to describe tangential series of ducts as traumatic and a scattered pine-like distribution as normal. Evidence has been presented (Thomson and Sifton 1925; Bannan 1936) which indicates that the various Abietineae form a graded series and that the ducts, whether in tangential series or of the diffuse type, are correlated with extraordinary environmental circumstances. The distinction between traumatic and so-called normal ducts is based upon an erroneous conception of the character of the traumatic tissue in the pines and related forms.

Although the distribution of ducts in the Abietineae is usually that described above, variation in different specimens may at times be so great as to render this criterion unreliable. For instance, the secondary xylem of seedling stems, the inner wood of branches, and the wood of certain vertical roots of *Picea* may possess no ducts, ducts in tangential series, or a few scattered vertical ducts and only widely separated horizontal ducts. In some cases the wood is like that in *Tsuga*, or at times approaches the condition in *Keteleeria*. In contrast, other specimens may have numerous ducts with a pine-like distribution. Consequently, on the basis of the distribution of resin ducts alone, occasions arise when it is difficult to distinguish *Picea* wood from *Tsuga*, or in other cases from *Pinus*. Under such circumstances, the identification of woods whose sources are unknown must be made with the assistance of other characters, as for instance the nature of the epithelium surrounding the ducts, the structure of the rays, or other features of the primary or secondary wood.

A peculiar type of tissue, probably traumatic in origin, was observed in a root of *Picea mariana*. It occurred in three growth rings: the sixth, ninth, and fourteenth from the center. In each the tissue was found in small groups arranged tangentially, in contact with the late-wood tracheids of the preceding ring on one side, and surrounded on the other three sides by semicircles of thick-walled parenchyma cells (fig. 4). The tissue was composed of thin-walled cells which stained deeply with haematoxylin but were unaffected by safranin. Since the outlines of bordered pits were discernible when the walls were viewed in radial sections, it is evident that the thin-walled cells were tracheids whose development had not proceeded much beyond the initial stages. Some resinous material was found in the areas. However, they differed from resin ducts in the absence of large intercellular spaces. In place of the extensive schizogenous cavities which characterize resin ducts there occurred incompletely developed tracheids.

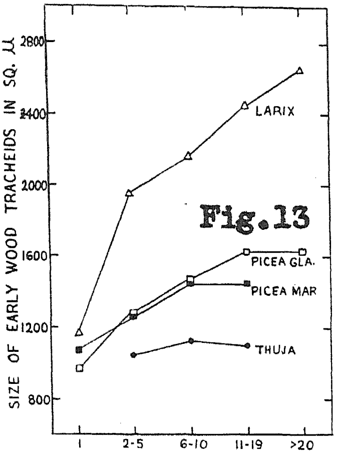
HEIGHT AND DISTRIBUTION OF RAYS

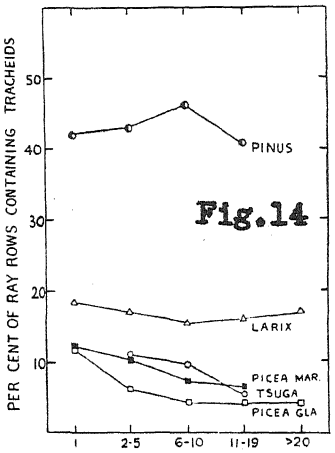
The average height of the rays in the inner wood of the lateral roots of adult trees is shown in figure 15 for five species of native conifers. In all the height was calculated at points 3 mm. from the primary xylem, two determinations being made for diarch roots, one on the radius paralleling the primary xylem plate, and the other on the radius at right angles to the plate. The determinations were made along the roots at the distances from the stem indicated in the figure. Different trends in ray height were observed. In *Thuja* the rays were low in the distal as well as in the proximal parts of the roots, but in the other conifers the height was greater, and as shown in figure 15, increased sharply with distance from the stem. When comparison was made with branch wood it was found that the average ray height in the distal roots of *Thuja* was approximately the same as in branches of like size and age, whereas in *Tsuga* the rays were slightly higher in roots than in comparable branches, and in *Picea*, *Larix*, and *Pinus* were much higher than in branches.

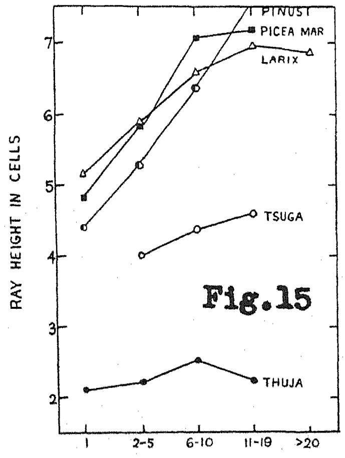
In diarch roots 1 cm. or less in diameter, the average ray height varied on different radii, being generally somewhat greater on the radii at right angles to the primary xylem plate. The growth rings also were usually wider in those radii, but on the whole no correlation between ray height and ring width was observed in roots of this size. The height in roots with wide rings generally was no greater than in roots with narrow rings. In this respect the roots differed from stems or branches of similar size. In the latter the rays were higher in the specimens with the wider rings (Bannan 1937).

The average ray height in the outer wood of large lateral roots, several cm. in diameter, varied greatly. In some roots it was about the same as that in the inner wood. In others there was a slight increase, and in yet other roots, especially where the outer rings became sharply narrower, some of the ray rows ceased and the average ray height declined. Generally the rays were slightly higher in the outer wood on the upper than on the under side, but occasionally the reverse was true.

No consistent relationship was discovered between ray height and soil conditions. In *Picea mariana* the average height was somewhat greater in







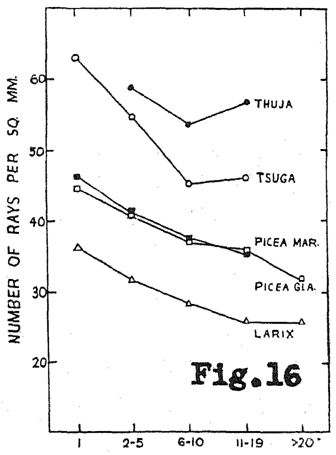


FIG. 13. Cross-sectional area of early-wood tracheids in lateral roots. The size of the tracheids was measured in the inner wood, 1 to 3 mm. from the primary xylem, and at the distances from the stem indicated. Data based on 174 sets of measurements. FIG. 14. Average percentage of ray rows containing ray tracheids in lateral roots. The percentage was determined at a distance of 3 mm. from the primary xylem; two calculations were made and averaged for diarch roots, one in the radial plane at right angles to the primary xylem plate, and the other in the plane paralleling the plate. Data based on 271 determinations. FIG. 15. Average ray height in lateral roots. The height was calculated at 3 mm. from the primary xylem, determinations being made from radial sections as described above. Data based on 295 determinations. FIG. 16. Average number of rays per sq. mm. of tangential section in lateral roots. The determinations were made at distances 3–5 mm. from the primary xylem. Data based on 263 calculations. The species are *Thuja occidentalis*, *Tsuga canadensis*, *Picea mariana*, *Picea glauca*, *Larix laricina*, and *Pinus Banksiana*.

roots growing in dry sand than in roots collected from swamps. A slight difference in the opposite direction was noted in *Larix laricina*, and in *Thuja occidentalis* and *Tsuga canadensis* no appreciable differences were observed between roots from these two types of habitat. These statements apply only to the smaller lateral roots, approximately 1 cm. in diameter. In larger roots of *Thuja occidentalis* the ray height in the outer wood was found to be greater in the drier habitats, but similar comparisons were not made for the other conifers. The range of variation between individuals on the same site was generally very much greater than the average differences between sites. At one site where a few roots of *Picea mariana* were collected from a very small area, the average ray height in one root was approximately double that in the others. The soil appeared to be uniform in texture and moisture content, and the trees were of similar size.

The number of rays per unit of tangential section, in lateral roots, was more or less inversely proportional to the ray height. In *Thuja*, where the rays were low, they were more numerous than in *Larix*, *Picea*, and *Pinus*, which had high rays (figs. 15, 16). Moreover in the latter genera the rays were less frequent in the distal parts of the lateral roots, where the height was greatest, than in the proximal portions. A factor in the lessening frequency of rays in the distal roots was the broadening of the tracheids which necessarily spread the rays farther apart.

The ray height in vertical roots (*Picea glauca*, *Pinus Strobus*, and *P. Banksiana*) was definitely lower than in lateral roots, and approximated the height in branches. The average height at 3 mm. from the primary xylem was 3.6 cells in *Picea glauca* and 3.8 cells in *Pinus Banksiana*, as compared with 5.5 and 5.3 cells in lateral roots the same distance from the stem. A like dissimilarity was noted in *Pinus Strobus*. Outward from the center of the roots the ray height increased slightly, but still remained below that in lateral roots. The average was 5 cells at 2–5 cm. from the primary xylem in vertical roots of *Picea glauca*, as compared with an average height of 6 to 7 cells in lateral roots of similar size, growing in the same kind of soil. In *Thuja occidentalis*, on the other hand, little difference was found between vertical and lateral roots, the average ray height being low in all roots.

Although different tendencies become apparent in various genera when a large amount of material is examined, both the height and distribution of rays vary too much from one specimen to another to be useful in differentiating closely related forms. For instance, the trends and average values in *Picea* and *Larix* are too similar to have any diagnostic value. Moreover the differences between individuals are much greater than the average differences between the two genera. The height and distribution of rays in *Thuja* differ markedly from the other conifers, but the wood of this genus may readily be separated from that of the Abietineae by other more reliable characters.

RAY STRUCTURE

The ray cells are principally parenchyma and tracheids, but the proportions of these cells differ greatly in various conifers. Ray tracheids were seldom found in the lateral roots of *Thuja*, they formed a small percentage of the ray tissue in the inner root wood of *Tsuga* and *Picea* (fig. 14), were more abundant in the roots of *Larix*, and made up from one-third to one-half the ray tissue in *Pinus*. In all genera ray tracheids were less numerous in lateral roots, particularly in the inner wood to a distance of 1 cm. from the primary xylem, than in stems or branches of similar size and age. The greatest difference between roots and stems was observed in *Picea glauca*, in which the proportion of ray rows containing ray tracheids was only 5 per cent in the inner wood of distal lateral roots as compared with from 20 to 40 per cent in stems; and the least difference in *Pinus* where ray tracheids were almost as abundant in some roots as in stems. The extent of these differences was indicated in a previous article (Bannan 1937), but it may be pointed out here that the values presented in that paper (table 1) for typical "buried" roots pertain to lateral roots only.

It is interesting to note that ray tracheids are usually slightly more numerous in stem wood of *Picea* (either *P. glauca* or *P. mariana*) than in *Larix* (*L. laricina*), but in roots the reverse is true. The proportion of ray tracheids in the inner wood of lateral roots of *Larix* was, on the average, twice that in *Picea* (fig. 14). In other words the degree of difference between root and stem was generally much greater in *Picea* than in *Larix*. This serves as another illustration of the manner in which conifers which closely resemble one another in many respects may differ markedly in the degree of reaction to similar environmental conditions in some other character. Relationships observed in one species are not necessarily of general application to the group as a whole.

Widely different proportions of ray tracheids were observed in the outer wood of the bigger lateral roots. In a large buttress root of *Picea Engelmanni*, examined at a point near the stem, ray tracheids made up 17 per cent of the ray tissue in the outermost rings on the upper side, but were absent on the under side. In another large lateral root, which was still 9 cm. in diameter at a distance of 12 feet from the stem, ray tracheids constituted less than 1 per cent of the ray tissue in the outer rings, both on the upper and under sides of the root. In other roots of *Picea Engelmanni* and in other species of *Picea* ray tracheids usually became more numerous in the outer rings. Thus in large lateral roots of *Picea glauca* and *P. mariana*, at distances from 1 to 10 feet from the stem, ray tracheids attained maximum values of from 20 to 30 per cent in the outer wood on the upper side, or nearly as much as in stem wood. In most roots ray tracheids were less numerous on the under side, the usual difference being from 5 to 10 per cent. Similar proportions were observed in the outermost rings in large lateral roots of *Larix laricina*. In *Thuja occidentalis* the percentage of ray tracheids was very low throughout the wood in lateral roots, averaging 0.3 per cent at 3 mm. from the primary xylem and 1 per cent at 1–3 cm.

In *Larix* ray tracheids were most numerous in roots obtained from the northern parts of the province. The average proportions were 20 per cent in northern Ontario and 13 per cent in southern Ontario (the determinations being made at 3 mm. from the protoxylem in lateral roots at distances from 6 to 19 feet from the stem). In both regions ray tracheids were slightly more abundant in roots growing in swamps than in dry sand, but the average differences were so slight as probably to be without significance. Similar differences between roots in wet and dry sites were observed in *Picea mariana*. On the other hand no appreciable differences between roots in varied habitats were discovered in *Tsuga canadensis*, and in *Thuja occidentalis* ray tracheids were scarce in all roots.

Wide variations in number of ray tracheids were noted among certain individuals of the same species growing under apparently similar conditions. For instance, in one tree of *Picea mariana* the average per cent of ray tracheids in the inner wood of lateral roots was 17, in another 6. Several roots were examined, but the deviation from the average was relatively slight in each tree, the roots of one having a consistently high proportion of ray tracheids (11–22 per cent), and the roots of the other a low proportion (4–10 per cent). The trees were of like size and were growing in an open coniferous stand on a sand plain. Although it cannot be stated that the environment was identical for both trees, no appreciable differences were detected in soil texture, moisture, or root competition. It would seem that these particular variations in number of ray tracheids were due to genetic rather than to environmental factors. Certainly the differences between individuals in the same habitat were much greater than the average differences between those from such unlike habitats as dry sand plain and swamp.

The proportion of ray tracheids in vertical roots, as a rule, was no higher than in lateral roots, and in some was lower. In vertical roots of *Picea glauca* ray tracheids made up 7 per cent of the ray tissue 3 mm. from the protoxylem in both lateral and vertical roots, but 2–5 cm. from the center ray tracheids were usually less numerous in vertical than in lateral roots. In the material examined the proportions 2–5 cm. from the center were 14 per cent in vertical roots and 22 per cent in lateral roots. In *Pinus Banksiana, P. Strobus,* and the western *Tsuga heterophylla* and *Pinus ponderosa*, ray tracheids were slightly less numerous in vertical roots up to 1 cm. in diameter than in lateral roots of corresponding size. Larger vertical roots of these species were not examined. In all roots of *Thuja occidentalis* ray tracheids were scarce.

It is noteworthy that although vertical roots have wood which is stem-like in so many respects (tracheid caliber, extensive late wood, arrangement of pits in the walls of the tracheids, and height of the rays), the ray tracheids not only have not taken part in this development of a stem-like wood, but, in some roots at least, have deviated in the opposite direction.

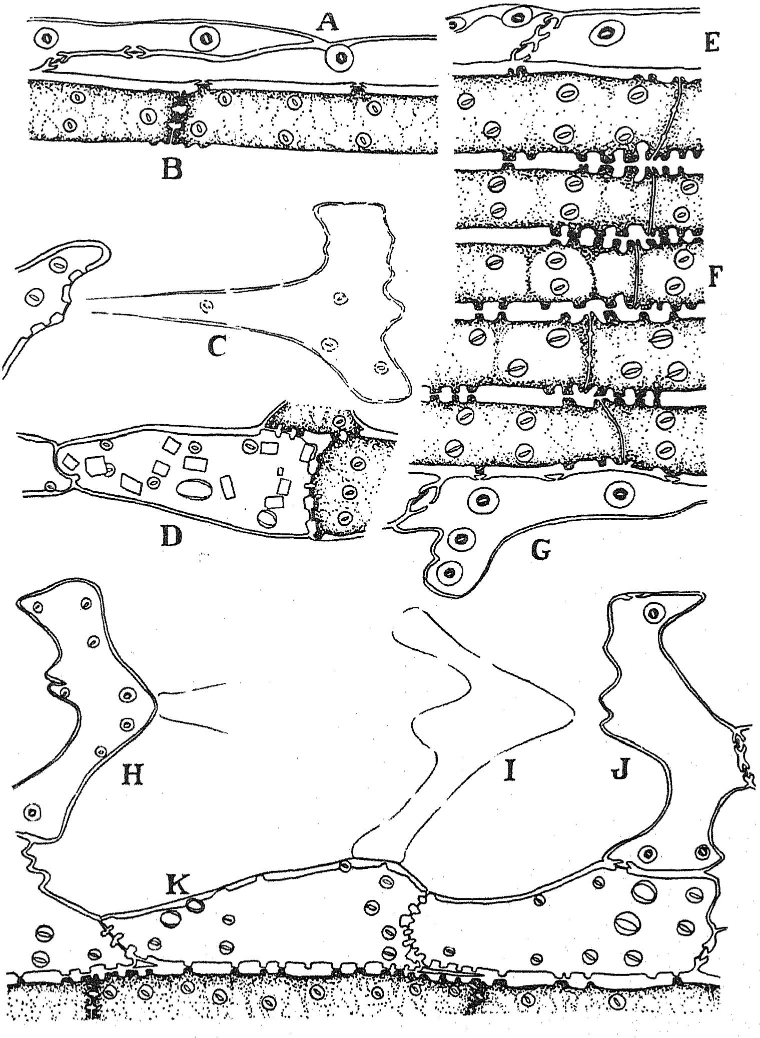


FIG. 17. *Larix laricina.* Types of ray cells in lateral roots. In the drawings of the parenchyma cells the pit apertures in the adjoining tracheids have been shown in addition to the margins of the simple pits in the walls of the ray parenchyma. Stippling represents protoplasm. Cells which are not stippled lack content, except in type D where crystals are present. Further descriptions in the text.

Ray tracheids were, in most of the specimens examined, slightly less numerous than in lateral roots of similar size, and were markedly less numerous than in comparable branch or stem wood.

In figure 17 are illustrated the different types of ray cells observed in the roots of *Larix laricina*. The ray parenchyma cells typically have thickened, lignified walls with simple pits. Between the pits are wall thickenings which sometimes have a knob-like appearance when viewed in radial sections (fig. 17, B, D, K). Occasionally these thickenings are much reduced, especially on the end or vertical walls (F). The protoplasm in the parenchyma cells usually persists for several years, but sometimes disintegrates early so that the cells appear empty (K) or contain crystals (D). The walls of the empty or crystal-containing cells may be very thin. The ray tracheids are devoid of protoplasm and have walls perforated by bordered pits (A and E). Some of the cells have vertical processes (G), and others, especially those near the origins of rays, are vertically elongated (H and J). The latter may have few pits, and these frequently are smaller (H) than in the more typical ray tracheids. Outlines of cells, known as ghosts, are occasionally to be seen near the points of ray origin or in the marginal rows of old rays (I). Sometimes the outline is a little more definite and small areas resembling pits can be recognized (C).

Although all the varied kinds of ray cell described above can sometimes be found in a single radial section, most of the ray cells are like types A and B. The other types occur rarely, but when present are usually to be found in new rays one or two cells high or in the marginal rows of the older, higher rays. The ray cells of *Tsuga* and *Picea* in general resemble those of *Larix*, though some minor differences were noted. For instance, the thinning of the end walls of ray parenchyma cells, shown in figure 17, F, was not observed in the roots of *Tsuga* or *Picea*. The ray cells of *Thuja* on the one hand and of *Pinus* on the other differ from those of *Larix* in some essential details which have been described or illustrated in other articles (Bailey and Faull 1933; Bannan 1934).

Certain features of the ray tissue are useful for differentiating coniferous woods. For instance, Bailey and Faull (1933) have demonstrated that the wall structure of the ray parenchyma cells distinguishes most Abietineae from the other conifers. Other features, however, such as the occurrence and proportions of the different types of ray cells are inconstant. Differences between genera or groups of genera observed in the majority of specimens, and which might accordingly be considered distinctive, sometimes disappear in other specimens or in certain parts of the tree.

On the basis of the ray cells in stem or branch wood the Abietineae may be divided into four rather ill-defined groups. In *Pseudolarix*, *Keteleeria*, and *Abies*, which may be considered as constituting one group, the rays are made up of varied proportions of the following types of cells: ordinary ray parenchyma, parenchyma cells with typical wall structure but devoid of content, ghosts, and very thin-walled cells with or without crystals. In material examined by the writer the differences between these three genera appeared to be quantitative rather than qualitative. Ghosts and crystal-containing cells were least numerous in *Pseudolarix* and most frequent in some species of *Abies*, but differences between individuals, parts of the tree, and possibly between species, especially of *Abies*, were such that it seemed doubtful if the woods of these conifers could be positively distinguished by their rays. Ray tracheids occur rarely in *Abies* but are too sporadic to have any diagnostic value. *Cedrus* resembles the foregoing in the presence of ghosts and crystal-containing cells, but differs in the general occurrence of ray tracheids. *Tsuga*, *Larix*, *Picea*, and *Pseudotsuga* constitute a third group of Abietineae in which ray tracheids are generally numerous, and ghosts, thin-walled cells, and similar types are relatively rare. Here again, however, the proportions of ray tracheids and parenchyma cells vary so greatly that this feature of the ray tissue does not provide a means of differentiating the woods of these four genera. In the genus *Pinus* some species have rays resembling those in *Picea*, while in other species ray tracheids are more numerous, the walls are further elaborated, and the ray parenchyma cells are also different.

The differences described above for stem or branch wood do not necessarily apply to root wood. For example, ray tracheids, although abundant in mature stem wood of *Picea*, are sometimes lacking in root wood. The problem of identification of the fossil woods is further complicated by the fact that the proportions of the various types of ray cells sometimes differed materially from those obtaining in their nearest living relatives. Ray tracheids are unreported in most fossil gymnosperm woods. These cells were observed by Arnold (1930) in certain species of *Callixylon*, and some tracheary cells of peculiar type have been described by Andrews (1940) for *Lyginopteris*, but generally the rays seemed to have been parenchymatous. Even in some of the Cretaceous pines ray tracheids occurred rarely or were lacking. These cells were not found in *Pityoxylon foliosum* and *P. anomalum* (Holden 1913), or in *Pityoxylon statenense* and *P. scituatense* (Jeffrey and Chrysler 1906). In *Pityoxylon scituatensiformis* (Bailey 1911) ray tracheids did not appear in the first 10–15 years' growth and were poorly developed in the subsequent wood.

In some fossil woods cells have been observed which, it was said, resembled or suggested ray tracheids but could not be positively identified as such. These indefinite cells have been reported in *Protopiceoxylon* by Seward (1919) and Read (1932). Stopes (1915) has illustrated for *Pityoxylon Benstedi* and *P. Sewardi* ray cells with simple pits in one wall and what were described as bordered pits in other walls. These cells were considered to be ray tracheids, but if cells have such mixtures of pits they obviously are not typical ray tracheids. Holden (1913), describing a Cretaceous *Pityoxylon*, noted cells along the margins of rays which were irregular in shape and destitute of resinous content. She stated that at first sight these cells appeared to be ray tracheids, but was careful to point out that the unbordered character of the pits negatived that possibility.

Irregular outlines, lack of content, and marginal position in the ray do not suffice to identify cells as ray tracheids. These characters are also common to certain parenchyma, thin-walled cells, ghosts, and other types which occur in varying proportions in the secondary xylem of living Abietineae. Only the presence of bordered pits exclusively can be considered an infallible criterion for establishing cells as ray tracheids. In radial sections this involves distinguishing between half-bordered pit-pairs, such as occur between tracheids and ray parenchyma cells in most Abietineae, and the full-bordered pit-pairs found between tracheids and ray tracheids. Since empty, irregularly shaped parenchyma cells, thin-walled cells, and other types occur in large numbers in certain living Abietineae, and are present to some degree in most genera, their occurrence is to be expected in fossils of Abietinean affinity. Possibly some of the indefinite cells reported in the literature are of these types.

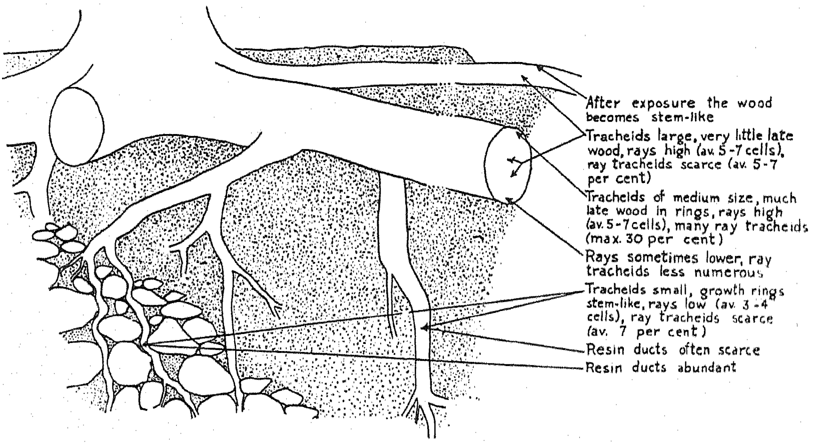

After exposure the wood becomes stem-like
Tracheids large, very little late wood, rays high (av. 5-7 cells), ray tracheids scarce (av. 5-7 per cent)
Tracheids of medium size, much late wood in rings, rays high (av. 5-7 cells), many ray tracheids (max. 30 per cent)
Rays sometimes lower, ray tracheids less numerous
Tracheids small, growth rings stem-like, rays low (av. 3-4 cells), ray tracheids scarce (av. 7 per cent)
Resin ducts often scarce
Resin ducts abundant

FIG. 18. *Picea glauca.* Schematic diagram of roots to show correlation between wood structure and location in the root system.

SUMMARY

A study was made of the secondary xylem in roots of native conifers to determine the range of structural variability within the species. Material was collected from varied habitats and from different parts of the root systems. The conifers investigated were the local species of *Thuja, Tsuga, Abies, Larix, Picea*, and *Pinus*.

A fine-textured, stem-like wood was found in the roots of small trees, in the upper side of buttress roots of mature trees, about the periphery of the largest lateral roots, in roots exposed by soil erosion, and in vertical roots deep in the soil. An open wood with large early-wood tracheids and little development of late wood was observed in the first one or two centimeters of growth in the distal parts of lateral roots located in the top few inches of soil (see fig. 18).

The diameter of the tracheids varied greatly in different parts of the root system, the greatest range being noted in *Larix,* the least in *Thuja*. No consistent relationship was discovered between tracheid size and soil moisture.

The pitting in the radial walls of the tracheids varied from opposite to alternate, the latter arrangement occurring most frequently in the inner wood of lateral roots of *Tsuga, Larix,* and *Picea*. Alternate pits were less abundant in *Thuja* and *Pinus*.

Vertical parenchyma cells were of erratic distribution in most of the genera studied. No trends were observed in different parts of the root systems.

The distribution of resin ducts was exceedingly variable. Ducts were most numerous in injured material, fewest in apparently unharmed specimens, for instance certain vertical roots penetrating deep into uniform sand. In such roots (*Picea glauca,* fig. 18) resin ducts were usually scarce, large areas of the wood possessing neither vertical nor horizontal ducts.

The height and distribution of rays varied greatly, both in different parts of the root systems and in different conifers. In general, the rays were highest and least numerous in the distal parts of lateral roots and lowest in vertical roots. The range of variation within the root system of a single tree was greatest in certain Abietineae, least in *Thuja*.

The proportions of the various kinds of ray cells (tracheids, parenchyma, and other types) varied throughout the root system and from one genus to another. The greatest variability was observed in *Picea* and the least in *Thuja*.

Because of this great variability in wood structure it is clear that anatomical studies must be based upon wide selections of material if they are to have taxonomic value.

The writer wishes to express his thanks to Professor R. B. Thomson for his interest in the work, and to Dr. D. H. Hamly for generous assistance with the photomicrographs.

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RAPID IDENTIFICATION OF THE MONTANE-SUBALPINE ZONE BOUNDARY[1]

RONALD L. IVES

(WITH ONE FIGURE)

In various parts of the Rocky Mountains, extreme difficulty has been experienced in making rapid, but reasonably accurate, differentiation between the montane and subalpine vegetative zones, which, in these areas, intergrade like the various minerals in a complex isomorphous series. This difficulty is further increased by the extreme irregularity of the zone of transition, a result of great local variations in water supply, temperature, soil, and effective solar radiation.

Where topographic relief is from slight to moderate, and soil and climatic conditions are reasonably uniform, zonal boundaries may be determined at a very few points, with any accuracy desired, and these findings extrapolated for considerable distances without introducing appreciable errors. Zonal definitions based solely on altitude are reasonably accurate in such areas.

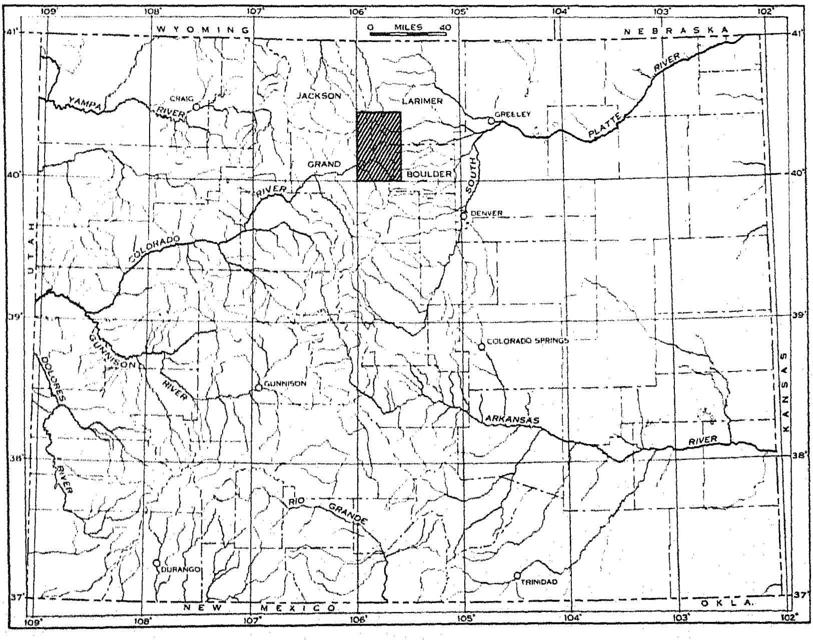

FIG. 1. Outline map of Colorado. Area of principal studies shaded.

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[1] Research assisted by grants from the Penrose Fund of the American Philosophical Society.

Altitude ranges of the various life zones in Rocky Mountain National Park, Colorado, are stated by Ashton (1, pp. 6–13).

Studies in the upper valley of the Colorado River (fig. 1), and in adjacent parts of the Front and Never-Summer Ranges, showed that extrapolations of more than a few thousand feet were hopelessly inaccurate in many areas. Complicating the biotic relations in this structurally and stratigraphically complex region are extreme local variations in climate, due in part at least to topographically-controlled convections (2) in the deep valleys carved into the mountain flanks during repeated Pleistocene glaciations.

Studies of plant successions in this area disclose that wherever montane forest cover has been removed, whether by lumbering, fire, avalanche or solifluction, the replacement growth is aspen (*Populus tremuloides*); and that where subalpine forest has been destroyed, replacement growth is limber pine (*Pinus flexilis*) in windswept areas, and predominantly lodgepole pine (*Pinus contorta*) where shelter is adequate. Montane and subalpine replacement growths tend to be mutually exclusive during the first few decades of reforestation, so that the dividing "line" between zones is relatively sharp.

Field investigations show that the transition from aspen to evergreen, as replacement growth, falls within the "zone of uncertainty" between the montane and subalpine zones. From these data, the following zone-identification criteria may be stated:

1. If replacement growth is wholly evergreen, the area is in the subalpine zone.

2. If replacement growth is predominantly aspen (80% or more), the area is in the montane zone.

3. In an area of considerable relief, where natural reforestation is in progress, and where the replacement growth is predominantly aspen at low elevations and wholly evergreen higher up, the transition from aspen to evergreen indicates the boundary between montane and subalpine forest.

4. Where replacement growth is mixed, with aspen not predominating, the area is in the montane zone, but the upper limit of aspen growth does not necessarily indicate the interzonal boundary, and may be far below it. This condition is common where reforestation is approaching completion, or where solifluction is in progress.

Rather obviously, these criteria may be applied rapidly, for aspen and evergreen growths are easily distinguished, even at a distance, either visually, or by use of infra-red photography (3). Areas undergoing reforestation can usually be identified without difficulty. Growths that are undeniably of the replacement type can be found in avalanche scars, which are most numerous on valley walls in the very localities where it is most difficult to distinguish between montane and subalpine forest by the usual methods, and where extrapolations from a few carefully-determined points tend to be least accurate.

These criteria appear sufficiently accurate for use in all but highly detailed studies in the Colorado Front Range area between latitudes 39° and 41°, and seem applicable southward to at least latitude 36°, as indicated by rough reconnaissances. Although they will probably be useful in many other parts of North America, either as stated, or with slight modifications, these criteria should not be depended upon, at any great distance from the Colorado Headwaters area, until they have been carefully checked, and their validity, for the area under consideration, definitely shown.

BOULDER, COLORADO

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CONTRIBUTIONS TO THE BIOLOGY OF POLYPORUS RHEADES (PERS.) FRIES

H. E. BAILEY

(WITH TWO FIGURES)

Polyporus rheades (Pers.) Fries is a common fungus in California, causing a destructive white-piped rot of oak.[1] The fungus is particularly common in the vicinity of Mount Diablo, Contra Costa County, California, where sporophores were found on several species of oak. *Quercus Wislizenii* A. DC., *Quercus lobata* Neé, and *Quercus Douglasii* H. & A. were those most severely attacked. Cross sections through the trunks showed most of those which were from three to four feet in diameter badly decayed, as well as many of the smaller ones (fig. 1).

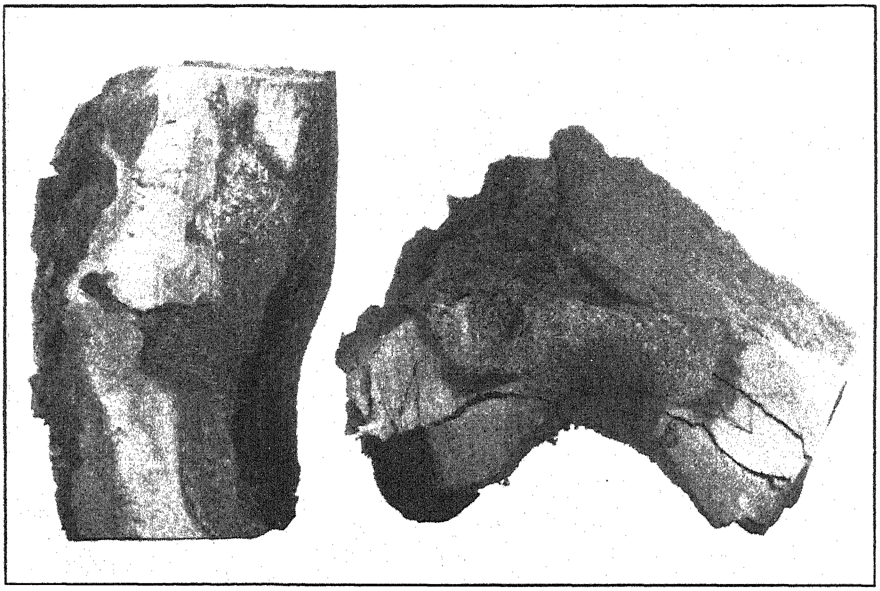

FIG. 1. Cross and longitudinal sections of a portion of a rotted trunk of *Quercus agrifolia* showing the typical mottled rot caused by *Polyporus Rheades*.

Sporophore formation occurs during the fall, usually between the months of September and November. The scarcity of sporophores at other seasons of the year may perhaps be explained by the fact that they are early attacked by insects. In the Mount Diablo region the fruiting bodies are disintegrated by a particular insect, *Tinea defectella* Zell., the larvae of which bore through the sporophore and honeycomb it with channels.

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[1] Hedgecock, G. G., and Long, W. H., Heart-rot of Oak caused by *Polyporus dryophilus* Berk. Jour. Agr. Res. 3: 65–80. 1914.

Sporulation in nature may be very abundant. In one instance it was noted that a deposit of spores 3–4 millimeters thick had collected under a sporophore which had grown in such a manner as to form a protective pocket between the pore surface of the sporophore and the bark of the tree. Freshly collected sporophores brought into the laboratory were very sensitive to changes in orientation and, in spite of precautions taken during transit from the field to the laboratory, the pore surface soon became covered with a new growth of mycelium. Shallow pores occasionally developed when these sporophores were kept under a bell jar, but sporulation never occurred from the newly formed pores. Sporophores produced in culture cast spores abundantly, some for a period of 30 days. The spores shed during this period in one culture weighed over 100 mg. (air dry weight).

Germination of the spores was erratic and the percentage low. Spores obtained from spore traps, spores shed directly onto the agar substratum, and spores produced from sporophores in culture were used in the germination tests. No germination occurred when the following substrata were used: plain 2 per cent agar, corn meal agar, malt extract agar, agar with 1 per cent phosphoric acid, or 1 per cent lactic acid, Leonian's agar, and oak agar. Spore germination was obtained, however, in a malt extract medium in which the mycelium had previously been growing. Drops of the filtered, sterilized medium were placed upon the lid of a Petri dish with sterile water in the bottom to keep the humidity high. These drops were then inoculated from a spore suspension. Examination showed about 15 per cent of the spores germinated.

In order to study the changes occurring in wood during the processes of decay, chemical analyses were made of samples taken from wood blocks which had been exposed to the fungus and which had lost 22.5 per cent, 29.7 per cent and 44.7 per cent in weight during successively longer periods of exposure to the fungus. The wood blocks were prepared as follows: a seasoned section of trunk of *Quercus agrifolia* nine inches in diameter was sawed into pieces one inch square and three inches long. These were soaked in water for one hour at reduced air pressure and then sterilized in an Arnold steam sterilizer on three successive days for a period of a half hour each. The blocks were then removed from the containers and placed on glass slides in previously prepared culture dishes in which a heavy mat of mycelium had been allowed to develop. In the preparation of these dishes a 2 per cent malt extract agar was inoculated with sporophore tissue.

The culture dishes containing the blocks of wood were kept in a humid chamber at 25° C. Color changes caused by the action of the fungus on the wood were early noticeable. The wood became progressively lighter in color and, in the most advanced stages, had a bleached appearance, with thin, dark, zone lines running irregularly through it (fig. 2). The rotted wood appeared stringy, was soft and spongy, and could easily be torn apart with the fingers.

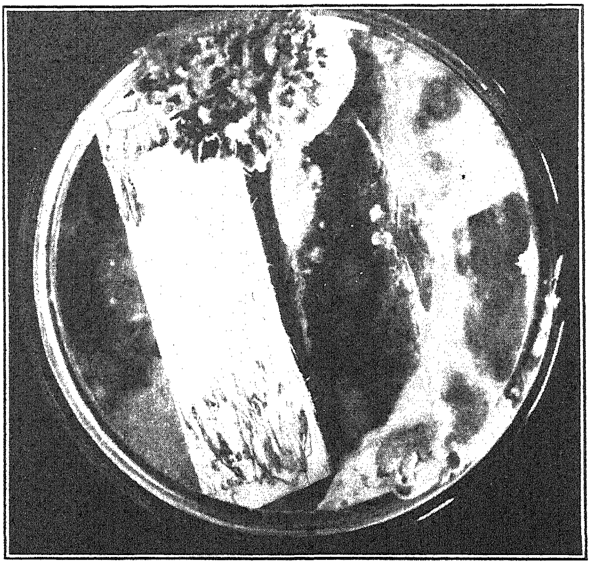

FIG. 2. Sporophore of *Polyporus Rheades* developed on wood block in culture. The dark zone lines in the wood are characteristic.

Samples of decaying wood were taken at various intervals during the exposure to the fungus, their loss in weight determined, and the components analyzed and compared with those of sound wood (table 1). Analyses were

TABLE 1

Chemical analysis of sound and decayed wood of Quercus agrifolia and tissue of Polyporus Rheades.

	Wood decayed in culture			Sound wood	Wood decayed in nature	Mycelium	Sporophore context
Loss in weight	22.5%	29.74%	44.7%		54.9%		
H_2O Sol.	9.22	9.09	6.77	15.65	4.33	17.52	13.85
Alc. Ben. Sol.	1.39	1.29	1.04	4.81	1.62	9.69	3.45
Cellulose	50.37	42.15	35.28	52.3	24.48	69.0	39.8
Lignin	10.81	6.46	6.90	20.8	15.42	55.0	60.8
Pentosans	15.50	14.50	12.0	22.6	7.53	2.37	0.777
Ash	0.868	0.95	1.12	2.34	0.889	0.945	0.217

also made of fungous tissue both from sporophores obtained in the field and from mycelium grown on wood blocks. Comparing the utilization of wood components by the fungus, we see that there is a progressively greater utilization of each of these in samples taken at successive intervals. The values obtained for the sporophore context and the mycelium differ appreciably from those obtained for wood.

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CALIFORNIA

INDEX TO AMERICAN BOTANICAL LITERATURE

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

Papers that relate exclusively to bacteriology, forestry, agriculture, horticulture, manufactured products of vegetable origin, or laboratory methods are not included. If users of the Index will call the attention of the editor to errors or omissions, their kindness will be appreciated.

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CHROMOSOME BEHAVIOR AT MEIOSIS IN TRIPLOID TRADESCANTIA HYBRIDS

NORMAN GILES

(WITH TWELVE FIGURES)

INTRODUCTION

A recent study of the chromosomes at the first post-meiotic mitosis in the microspores of diploid species of *Tradescantia* L. has demonstrated the rather frequent occurrence, especially in hybrids, of spontaneous chromosome changes (Giles 1940). A similar examination of the chromosomes of triploid *Tradescantia* hybrids has shown the same types of post-meiotic changes. It has also been found that other types of aberrations, resulting from meiotic irregularities, occur at the pollen grain mitosis. To aid in interpreting and distinguishing these two classes of aberrations, a study has been made of chromosome behavior at meiosis. The actual types of aberrations revealed at the first post-meiotic mitosis will be described and discussed in the second part of this study (Giles 1941). The present observations at meiosis have also provided material for an analysis of the comparative amounts of structural hybridity of the chromosomes in the diploid and tetraploid parents and in the triploid hybrids between them, and this paper deals in large part with a discussion of this subject. Since it has recently been shown that heterozygous inversions may occur with considerable frequency in species of *Tradescantia* (Sax 1937; Darlington 1937a; Swanson 1940), particular attention has been paid to evidence for inversion hybridity.

MATERIALS AND METHODS

The triploid plants used in this investigation were the result of a cross between a diploid *Tradescantia paludosa* Anders. and Woods. as female, and a tetraploid *T. canaliculata* Raf. as male parent. The *T. paludosa* stock was originally obtained by Dr. Edgar Anderson at Gentilly, Louisiana, some years ago, and a clone from this material is maintained at the Harvard Biological Laboratories. The *T. canaliculata* was collected by the writer near Atlanta, Georgia, in the spring of 1938. The two parents are quite typical of their respective species, and show no evidence of having hybridized with

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other species in the field. In their external characteristics the hybrids give almost no indication of being intermediate between the two parents. It is true that the parental species do not differ greatly to begin with, but even of those characters in which they are different, such as the distribution of stomata, shape and size of bracts and leaves, general habit of plant, and hairiness of leaves (particularly the lower leaf sheaths, and entire young leaves), the hybrids tend to exhibit almost all the characters of *T. canaliculata.* This is very probably due to the presence in the hybrids of two sets of genes from *T. canaliculata* and only one from *T. paludosa.* It is interesting to note that hybridization under natural conditions involving these two species and *T. hirsutiflora* Bush, with the occasional production of triploids, has been reported recently by Riley (1939).

In the cytological study of the plants, aceto-carmine smears of meiosis were used.

CHROMOSOME BEHAVIOR AT MEIOSIS

A comparative study has been made of chromosome behavior at meiosis in the three types of plants studied, with particular emphasis on the various types of aberrations due to structural hybridity. Of these, inversion bridges are by far the commonest, and their frequencies in the parental types and the hybrids were found to differ considerably. The types of chromosomal configurations in the three groups and their relation to chiasma frequency and inversion bridge frequency have also been considered.

Pairing Relations and Chromosome Distribution. Meiosis in the diploid *T. paludosa* is very regular. The only irregularity in pairing noted was the occurrence of 4.3 per cent univalents at metaphase. Despite the presence of a certain number of univalents, chromosome distribution is very regular, for in 128 cells scored only 6–6 distributions were noted. Also in the same cells no lagging chromosomes were noted (table 1). The chiasma frequency is fairly high, 2.4 per bivalent, of which one-third are interstitial.

Meiosis in autotetraploid tradescantias is characterized by the occurrence of quadrivalents and trivalents as well as bivalents and univalents. In the plant of *T. canaliculata* studied, the frequency of quadrivalents was 2.7 per cell and of bivalents, 5.1 per cell (table 1). This is somewhat lower than usual, for in most tetraploid tradescantias studied the frequency of quadrivalents per cell has been at least three (Darlington 1929; Anderson and Sax 1936). This lower percentage of quadrivalents may be due to the somewhat lower chiasma frequency, 0.7 per chromosome, as compared with 0.8 and 0.9 for plants with more quadrivalents. The increased percentage of bivalents may mean that the chromosome complement was derived from two gametes quite unlike in the structure of their chromosomes. If the resemblances as to pairing properties of chromosomes were closer within each set than between the two sets, we should expect a higher proportion of bivalents. That a situation with similar results may indeed arise has been shown recently by Skirm (1940). He found that doubling the chromosome number of a hybrid *Tradescantia* resulted in a tetraploid with an extremely low frequency of quadrivalents. Here the four chromosomes sets present existed as two identical sets which apparently differed sufficiently from one another to condition synapsis almost exclusively as bivalents. In distribution the chiasmata studied in the present plant agreed with findings for other autotetraploid tradescantias in being almost all (99.3 per cent) terminal. The distribution of chromosomes was rather irregular because of variations in quadrivalent and trivalent orientation and the random passage of univalents to the poles. Also the amount of lagging was rather high. Of 263 cells counted, lagging chromosomes were present in 58, or 22.1 per cent.

Meiosis in the triploid hybrids was much more irregular than in either of the two parental plants. Five plants were studied in detail and the data (averages) on chiasma frequency and types of configurations in these are presented in table 1. The plants did not vary much in the relative number of univalents, bivalents, and trivalents per cell, or in their chiasma frequency. The average number of trivalents for the five was 3.6 per cell. This is considerably less than that found in an autotriploid plant of *T. bracteata* Small with a frequency of 4.64 (Sax 1937), and is evidently related to the hybrid nature of these plants, since they have two sets of *T. canalic-*

TABLE 1

Pairing configurations and chiasma frequencies in diploid T. paludosa, tetraploid T. canaliculata, and triploid hybrids.

Plant	Number of cells	I	II	III	IV (Also V & VI in 3n's)	7 configurations in one cell (3n)	Total Xta	Xta per chromosome	Terminal Xta per cent	Interstitial Xta per cent
T. paludosa	30	8	176	....	....	......	440	1.2	66.4	33.6
(2n)	per cell:	.27	5.87	....	....	......	14.7			
T. canaliculata	85	97	435	47	233	......	1532	.75	99.3	.7
(4n)	per cell:	1.1	5.1	.5	2.7	......	18.0			
3n hybrids	307	678	712	1104	26	13	4053	.73	90.1	9.9
(averages for 5 plants)	per cell:	2.2	2.3	3.6	....	......	13.1			

ulata chromosomes and only one of *T. paludosa*. That all the chromosomes are largely homologous is shown by the observation of a number of cells with six trivalents (fig. 1).

Of particular interest in obtaining an estimate of the amount and nature of structural hybridity in these plants are the observations on unusual pairing configurations at metaphase. Such configurations were encountered only in the triploids, but this is to be expected as a result of the modified method of pairing due to the presence of an extra set of chromosomes, as well as to their hybrid origin. Failure to observe them in the diploid and tetraploid does not prove the absence of the types of hybridity which they indicate. The observed configurations indicate the presence of translocations between, or duplications in, non-homologous chromosomes, and duplication in different arms of the same chromosome. It is not possible in these plants to distinguish between translocations and duplications since the observed configurations might result from either condition. The types of synapsis which indicate translocations and duplication are multivalents and a total of more than six distinct configurations in one cell (fig. 2). The majority of the multivalents are quadrivalents (fig. 3), but occasional associations of five and six chromosomes have been observed. The presence of more than six configurations in a cell indicates intra-haploid pairing and shows that homologous segments are present in non-homologous chromosomes. These two types of irregularties in pairing have been observed in approximately 12.5 per cent of the sporocytes examined. The evidence for

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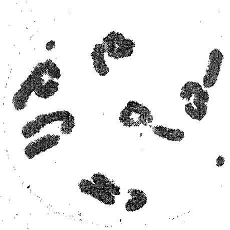
Explanation of figures 1–12

Configurations observed at metaphase and anaphase of meiosis in the triploid hybrids. ×660. FIG. 1. Cell containing six trivalents at metaphase. FIG. 2. Metaphase with seven paired configurations, indicating intra-haploid pairing; two univalents also present. FIG. 3. Quadrivalent pairing at metaphase (lower left). FIG. 4. Metaphase showing ring of three with interstitial chiasma (left center), indicating duplicated segments in differing arms of the same chromosome. FIG. 5. Four inversion bridges in the same cell at anaphase I. Centric and acentric fragments present. FIG. 6. Bivalent with inversion bridge in each arm (to left); small acentric fragments out of focus. Also single bridge and acentric fragment to right. FIG. 7. Two bridges connecting all three chromosomes of a trivalent at anaphase. One acentric fragment in middle of cell at right; two centric fragments at opposite poles to left. FIG. 8. At left center, univalent bridge resulting from precocious division of centromere at anaphase I; acentric fragment out of focus directly above bridge. Also single bridge at right center, and dividing univalent at left. FIG. 9. At lower right, loop chromatid and acentric fragment resulting from single crossing-over within an inversion. Precocious division of the centromere of such a chromosome would give a univalent bridge as seen in figure 8. FIG. 10. Three inversion bridges having acentric fragments (indicated by arrows) all of different lengths. The small one on the right is apparently attached to the end of a free arm. Three centric fragments are also present. FIG. 11. Single bridge in cell at right at anaphase II, resulting from a loop chromatid at anaphase I as seen in fig. 9. The acentric fragment present in the spindle was evidently included in the nucleus at anaphase I. FIG. 12. Bridge and acentric fragment resulting from inversion crossing-over in one of the small centric chromosomes often present in *Tradescantia*.



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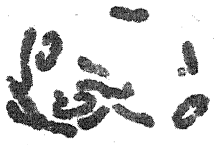

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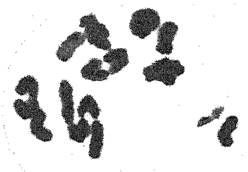

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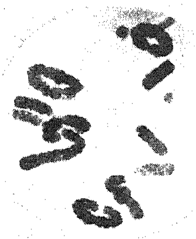

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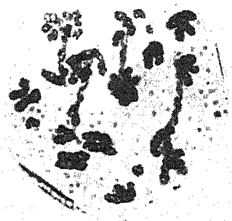

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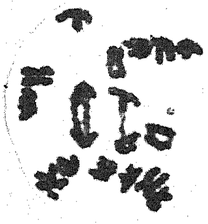

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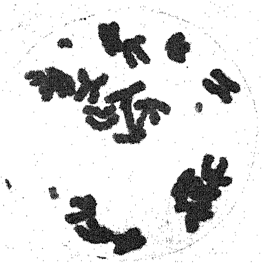

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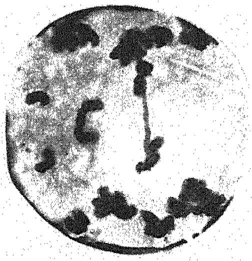

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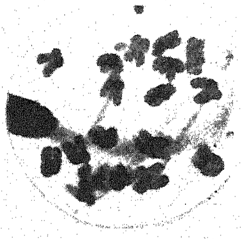

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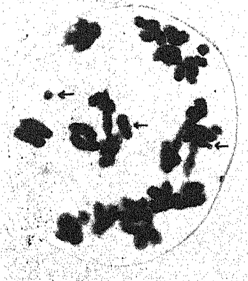

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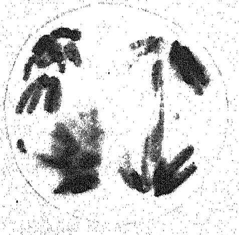

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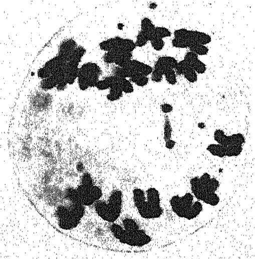

12

duplications in different arms of the same chromosome is obtained from the occasional observation of configurations typical of secondary trisomics (Belling 1927). Two of these which were noted occasionally are rings of three and univalents paired back on themselves. In the rings of three, one chiasma was usually interstitial, indicating the probable interstitial position of the duplicated segment (fig. 4). These two configurations are quite rare, and have been found in only about 2.5 per cent of the cells examined.

The comparative rarity of these unusual configurations shows that the structural changes which they indicate are relatively few and probably quite small. It is only the presence of unpaired regions as a result of the extra set in the triploid that permits detection of them. The resulting configurations are of interest in an interpretation of some of the aberrations noted at the microspore division, which will be discussed in the second part of this study (op. cit.).

Chromosome distribution at first anaphase in the triploids was quite irregular, as is indicated by a study of 158 cells (in two different plants) of which 107 (67.7 per cent) contained lagging chromosomes. Precocious division of univalents occurred commonly, but no misdivision of the centromere, as observed by Upcott (1937a) in *Tulipa* L. and Darlington (1939, 1940) in *Fritillaria* L., was noted.

Centric fragment chromosomes were present in all the triploids, the diploid, and the tetraploid. Particularly in the triploids, they were observed to pair with the larger chromosomes, indicating their homology with certain of these.

Heterozygous Inversions. The frequency, types, and behavior of inversion bridges at both anaphases I and II were studied in the two parental forms and in six of the F_1 hybrids. The data are presented in tables 2 and 3. In the diploid only single bridges were noted at A I (in 5.7 per cent of the cells). About half of the dicentric chromatids are without visible acentric fragments, as has been noted before for inversion bridges in *Tradescantia.* Most of the visible fragments are approximately spherical; that is, they are about as long as the width of a meiotic chromosome arm. However, occasional smaller or larger fragments are noted, indicating the presence of more than one inversion. Since all centromeres are approximately median, individual chromosomes cannot be distinguished, and it is impossible to determine whether the different inversions are in the same or in different chromosomes. The latter is quite probably the case, since, although the chiasma frequency is high, no double bridges involving either one or both arms of a single chromosome have been observed. In the tetraploid the frequency of bridges on a cell basis was 18.5 per cent. Six cells of 281, or 2.1 per cent, had bridges in two different chromosomes. Here again approximately half the bridges were without fragments. In those cells where fragments were present these were

TABLE 2

Bridges at anaphase I of meiosis in diploid, tetraploid, and triploids.

Plant	Number of cells	Number of cells with different numbers of bridges & percentage					Total number of bridges	Per cent bridges
		0	1	2	3	4		
T. paludosa (2n)	335	316 94.3	19 5.7	....	....	....	19	5.7
T. canaliculata (4n)	281	235 83.6	40 14.3	6 2.1	....	....	52	18.5
3n hybrids (average per cent for 6 plants)	1015	646 64.7	308 30.8	52 3.65	8 .73	1 .15	492	40.9

TABLE 3

Bridges at anaphase II of meiosis in diploid, tetraploid, and triploids.

Plant	Number of cells (not tetrads)	Number of cells with different numbers of bridges & percentages				Total number of bridges	Per cent bridges
		0	1	2	3		
T. paludosa (2n)	194	190 97.9	4 2.1	....	....	4	2.1
T. canaliculata (4n)	300	290 96.7	9 3.0	1 .35	....	11	3.7
3n hybrids (average per cent for 6 plants)	1494	1368 91.1	120 8.5	6 .4	....	132	9.3

almost all small, only one as long as the width of a chromosome arm being noted. This seems to indicate that most of the inversions (at least those in which crossing-over occurs) are close to the ends of the arms. The frequency of bridges observed is much higher than any hitherto recorded in tetraploid tradescantias. Darlington (1937a) states, without giving specific examples or figures, that bridges occur in less than one per cent of the cells of tetraploid tradescantias and are less frequent than in diploids. It is possible that the higher percentage found in the present plant may be related to the higher frequency of bivalent pairing, although it seems more likely that such pairing would reduce the bridge frequency since regular pairing in small inversions would presumably not be facilitated. Bridges at anaphase II were noted in 3.7 per cent of the cells studied (7.4 per cent of the tetrads).

The frequency of bridges in six plants of the hybrid triploid population varied somewhat. However, the plants were all alike in having a considerably greater frequency of bridges per cell than either of the parents. The higher frequency holds for both first and second anaphase, and is reflected in the much greater percentage of cells with more than one bridge. As many as four bridges in different chromosomes were observed in a single cell (fig. 5). Certain configurations also show that two inversions may be present in the same homologous chromosome. These may be in the same arm or in different arms. If crossing-over occurs in two heterozygous inversions located in opposite arms of a paired bivalent, the configuration shown in figure 6 will result. Similar behavior involving a trivalent instead of a bivalent results in a V-shaped association (fig. 7). The latter type has been observed several times. When two separate inversions are located in the same arm, complementary crossing-over in both of these results in unequal bridges with two acentric fragments of different lengths. Such a figure has been observed only once. The other possible types resulting from reciprocal and disparate crossing-over in the two inversions—respectively a single bridge plus an acentric ring and acentric fragment, and a single bridge and acentric fragment plus a very long free chromatid arm—have not been noted. These same types could also be produced by crossing-over in overlapping inversions (cf. Swanson 1940). One cell with two bridges of equal length in the same arm and equal acentric fragments was found. This condition is due to double crossing-over within a single inversion. The rarity of such configurations is due both to the low chiasma frequency in the triploids and the probable short length of most of the inversions. The frequency of bridges at anaphase II in the triploids is also rather variable and shows no constant relation in individual plants to the frequency at first anaphase. As has been pointed out by Upcott (1937b) this is due to the peculiar chromosome behavior of triploids. Of the four factors cited in her paper as important in triploid tulips, two seem to be of particular import in triploid tradescantias: non-disjunction, and precocious division of univalents. The passage of both centromeres of a dicentric chromatid to the same pole at first anaphase may give rise to a bridge at the second division, or if the separation is parallel the dicentric will be recovered in the microspore. Of the total of 430 dicentric bridges observed in the five triploids studied, 30 (7.0 per cent) were passing to the same pole. The precocious splitting of unoriented univalents which have undergone inversion crossing-over results in the occurrence of univalent bridges (fig. 8). Such behavior increases the frequency of bridges at the first division, but since they can be recognized an idea of their frequency can be obtained. In a count from plant 1, of a total of 80 bridges of all types, 7 (8.7 per cent) were univalent bridges. This seems to indicate that the frequency of non-disjunction and univalent bridges is about the same. However, no adequate records were kept for other plants, and it is possible that the frequency of univalent bridges is too high in the sample cited. Most of the bridges at the second division are due to crossing-over within and proximal (disparate) to an inversion. These are evident as loops attached to one centromere at one pole at first anaphase (fig. 9) and are observed quite often.

The visible acentric fragments in the triploid vary a great deal in size, giving further evidence for the presence of numerous different inversions. Figure 10 shows three bridges, all having fragments of different sizes. These fragments rather often appear to be attached to the free arm of a chromatid at anaphase (fig. 10) as has been found in *Zea* L. (McClintock 1938) and consequently may be included in the nucleus at telophase I. Their inclusion is further indicated by the presence of occasional cells with fragments in the spindle at anaphase II (fig. 11). That only very few of these are ever included in the nucleus at telophase II will be shown later (Giles 1941). It has also been found that the centric fragment chromosomes in these plants may contain inversions in which crossing-over occurs, as has been noted by Swanson (1940) in a diploid *Tradescantia.* In 299 cells of plant D a bridge in the fragment chromosome, usually with accompanying acentric fragment, was present in 26, (8.5 per cent; fig. 12). The data for the centric fragments are not included with those for the normal chromosomes.

Quantitative Estimation of Hybridity. In an endeavor to obtain some idea of the nature and amount of structural hybridity in the two species and in the hybrid between them, there are three methods of approach, all of which may be used to advantage. In the first place, by observing the pairing relations at metaphase we can determine if reciprocal translocations or duplications (at least in the triploid) are present. The evidence for these, i.e., the unusual configurations in the triploids, has been discussed. It seems clear that duplications are present, although they are undoubtedly small and not very numerous. No configurations indicative of duplications have been noted in the diploid and tetraploid, but, as has been previously pointed out, it is impossible to say that none are present. It is clear that there are no large heterozygous reciprocal translocations in any of the plants, for the expected constant multivalent configurations are absent.

The second and third methods are particularly concerned with determining the amount of inversion hybridity. The most obvious method is to attempt to identify at anaphase I of meiosis specific inversions as shown by their presence in particular chromosomes and by the size of the fragments released, since a single crossover at any point in a given inversion will always release a fragment of the same length. If the chromosomes are individually distinguishable this may be possible. When, however, they are all of about the same size and shape as in the present plants, the method is not so simple. However, it is possible to obtain a reasonably accurate estimate of the minimum number of inversions by taking into account the greatest number of bridges noted in any one cell, as well as the sizes of the fragments present. In the diploid plant not more than one inversion bridge in any one cell was noted. However, the size of the fragment varies. Although most of the visible fragments are about as long as the width of a meiotic chromosome, occasional smaller or considerably longer fragments occur. This indicates that there are at least three different inversions present. In the tetraploid plant cells were observed with two inversion bridges, the fragments of both being about the same size. Also, as has been mentioned earlier, there were two classes of visible fragments. With this evidence we can say that at least three inversions are present in the chromosomes of the tetraploid. Since, however, we are dealing with four homologous chromosomes in each cell, whose total pairing length is twice that of the diploids, this does not mean that all of the inversions are qualitatively different; that is, that they involve the rearrangement of non-homologous genes. We actually have evidence for only two qualitatively different inverted sequences, since the cells with two bridges having equal fragments may have resulted from crossing-over within two homologous inversions. This difficulty in recognizing qualitatively different inversions does not arise in the triploids in which the pairing length of the three homologous chromosomes is the same as in the diploid. Although it is true that some of the bridges observed in the triploids may be the result of crossing-over following chromosome pairing in aberrant configurations other than heterozygous inversions, it is still at once obvious that we have evidence for many more inversions than in either of the parents. Four bridges were noted in a single cell. We also know that at least one chromosome has an inversion in both arms. Further, the occurrence of a double bridge in one arm with fragments of two different sizes indicates the presence of two separate inversions in one arm or two homologous arms. Consequently, we are justified in assuming a minimum of six different inversions in the triploids.

Obviously, the method just outlined cannot give us an accurate measure of the degree of inversion hybridity, but only an idea of the minimum number of inversions present. A method for obtaining a general quantitative estimate of the total amount of inversion hybridity is that suggested by Darlington (1937b) and termed a *coefficient of hybridity*. This value is obtained by adding together the frequencies of inversion bridges per pollen mother cell and dividing by the average chiasma frequency per cell. It is also necessary in calculating the frequency of bridges to count all double bridges at the first division which result from crossing-over within the same inversion as six instead of two, since, as Darlington points out, these are the result of complementary crossing-over and presumably represent equal numbers of reciprocal crossovers which will not give bridges and disparate crossovers which give only one bridge instead of two. In the present plants, however, we need not consider this latter point, since the only case of double crossing-over within an inversion was on a slide not included in the data presented.

The result of these calculations for the present group of plants is indicated in table 4. As was pointed out, the frequency of bridges is that observed per pollen mother cell, not per cell. Consequently, the values for the percentages of bridges at anaphase II in table 4 are twice those in table 3.

TABLE 4

Comparative bridge frequencies at anaphase I and II of meiosis in diploid and tetraploid tradescantias and triploid hybrids between them. Calculation of coefficient of hybridity for inversions.

Species	Bridges A I	Bridges A II	Total bridges (Inversion C.O. frequency)	Average Xta per cell	Coefficient of inversion hydridity (cell basis)	Corrected to chromosome basis
T. paludosa (2n)	.057	.042	.099	14.7	.0067	.0067
T. canaliculata (4n)	.185	.074	.259	18.0	.0144	.0072
3n hybrids (average of 6 plants)	.409	.186	.595	13.1	.0454	.0302

Before considering the results obtained, let us first examine the limitations of this method as applied to the present case. Actually the method as outlined is generally applicable only to diploids with a random distribution of chiasmata. Consequently, we are immediately faced with two difficulties, since we are studying triploids and a tetraploid as well as a diploid, and, further, since there is some evidence that crossing-over in diploid tradescantias may be restricted in regions of the chromosomes adjacent to the centromeres.

In order to compare the relative amounts of inversion hybridity in the chromosomes of the diploid and the tetraploid, it is clear that the percentage of bridges should be given on the basis of chromosomes rather than cells. Consequently, we must divide the total percentage of bridges in the tetraploid by two. A further difficulty arises because each chromosome is represented four times in the cells of the tetraploid and consequently the pairing length of homologous chromosomes is potentially twice as great in the tetraploid as in the diploid. For any four homologous chromosomes the gene sequence may be the same in all four, or different in one, two, or three. When the sequence in one of the chromosomes differs from that in the other three, the result of crossing-over will be the same as that in the diploid, unless the chromosome having the inverted sequence fails to pair, in which case the bridge frequency would be reduced. The same conditions would hold when three chromosomes have an inverted sequence and one is normal. The condition which might produce a considerable difference in bridge frequency in the tetraploid as compared to the diploid is that in which two of the chromosomes have a normal and two an inverted sequence. In such a case preferential pairing between chromosomes having similar sequences may occur, which would reduce the frequency of inversion bridges. However, pairing among the four chromosomes may also be at random. If this occurs, inversion pairing will be present in only four out of the six possible associations. However, in a diploid with a corresponding degree of inversion hybridity, that is, one inversion in one homologous pair, there is no possibility under normal pairing conditions of non-inversion pairing. In consequence, under such circumstances (when there are two identical inverted sequences in two of the four homologous chromosomes) the observed bridge frequency in the tetraploid should be increased by 33 per cent in order to correct for this reduction in bridge frequency due to the type of pairing. It is not possible to ascertain, however, how often when two bridges occur in one cell we are dealing with such identical inverted sequences in homologous chromosomes. It is probable that the fraction would be a rather small one. At any rate these considerations, and those pointed out earlier, indicate that the amount of hybridity as indicated by the percentage of bridges in the tetraploid is certainly a minimum estimate.

In comparing the data for the diploids and triploids certain corrections must also be made. Here again the comparison should be made on the basis of chromosomes rather than of cells. To do this the observed percentage of bridges must be divided by 1.5 since one bridge represents one inverted sequence in 18 chromosomes in the triploid as compared with one in 12 chromosomes in the diploid. The linear order of the homologous sequence in the extra chromosome in the triploid makes no difference since it must be similar to that of one of the other two chromosomes and the percentage of inversion hybridity remains the same in either case. This is true provided the three chromosomes do not differ by inversions involving different breakage points within the same region. Since most of the inversions appear to be small ones, this possibility seems rather unlikely, but it cannot be excluded. The possibility of preferential pairing must also be considered in the triploid. This is especially true in the present plants since we are dealing with what are basically allopolyploids, having two sets of chromosomes from *T. canaliculata* and one from *T. paludosa*. However, the evidence from metaphase pairing indicates that all three sets are largely homologous, since the behavior is that of autopolyploids with somewhat reduced trivalent formation. In triploid *Drosophila melanogaster* females heterozygous for one inversion, the evidence indicates that the two normal chromosomes conjugate and pass to opposite poles more often than would be expected on random distribution, suggesting that pairing of the chromosome having the inversion is reduced (Sturtevant 1931). In *Tradescantia*, however, since the evidence indicates that crossing-over in diploids may be largely restricted to the distal regions of the chromosomes, the presence of an extra chromosome, even one containing an inversion, would presumably facilitate the association of most of the regions in the chromosome. This should increase the amount of inversion crossing-over, especially if any inversions are located in the regions proximal to the centromere, as recent evidence indicates (Swanson 1940). To believe, however, that the great increase in frequency of bridges in the triploid hybrid plants is due entirely to the type of pairing does not seem warranted. Evidence as to how much the type of pairing in the triploid may be responsible for this increase is obtained from the results on an autotriploid *T. bracteata* (Sax 1937). Here the frequency of bridges at A I was only 16.3 per cent. No data are presented for A II. Since in the autotriploid we have two sets which are identical or nearly so, we should expect the bridge frequency to be even less than in the diploids. If inversion crossing-over coefficients for this plant (for A I) and the average diploid (with approximately 5 per cent bridges) are calculated, the triploid value is approximately three times that of the diploid. In hybrid triploids, however, this increase is about seven times that of the diploid. This must indicate that a considerable part of the increased bridge frequency of the hybrids is due, not to the type of pairing, but to a greater amount of structural hybridity, as would be the case if the sequences contributed by the parents are different. Since the percentage of interstitial chiasmata in the diploid is considerably higher than the average for the triploids and also for the tetraploid (table 1), the calculated inversion hybridity coefficient for this plant should tend to be higher than those for both of the tetraploid and the triploids if inversions are more common in the regions proximal to the centromere (cf. Swanson 1940). It is also true that other anomalous types of pairing in the triploids, such as intra-haploid pairing between relatively inverted segments, may lead to the formation of bridges, and this is another reason why the coefficient of inversion hybridity for the triploids does not have the same validity for comparative purposes as it does for diploids.

As a result of the above considerations, it seems clear that, although the method of calculating coefficients of hybridity for inversions cannot be applied without considerable modification to the comparison of different species of tradescantias in which polyploidy is present, it does permit certain conclusions. These are that the amount of inversion hybridity is least in the diploid *T. paludosa* and somewhat higher in the tetraploid *T. canaliculata* used in this study. Furthermore, it seems clear that the gene sequences of homologous chromosomes within each of the plants of the two species studied resemble each other more than do the sequences of homologous chromosomes of their hybrid. In other words, in this case the difference in gene sequences is less within an individual of one species than between individuals of two different species.

SUMMARY

A comparative study has been made of the behavior at meiosis of the chromosomes in a diploid *Tradescantia paludosa*, an autotetraploid *T. canaliculata*, and in a number of the triploid hybrids resulting from a cross of these two plants. Certain configurations observed in the triploids, though comparatively rare, indicate the presence of small translocations between, or duplications in, non-homologous chromosomes, and duplication in different arms of the same chromosome. These configurations have not been observed in the diploid or in the tetraploid, but their absence in these plants does not prove the complete absence of the types of hybridity which they indicate. There was no evidence of large heterozygous reciprocal translocations in any of the plants examined. Heterozygous inversions, as indicated by the presence of dicentric bridges and acentric fragments, were present in all the plants studied. The types of bridges and their frequencies in the different plants are described. The various difficulties encountered in making a quantitative estimate of inversion hybridity for comparative purposes in these plants, particularly in the triploids and the tetraploid, are discussed. It is concluded that on a chromosomal basis inversion hybridity in the particular plants used in this study is least in the diploid *T. paludosa*, somewhat greater in the tetraploid *T. canaliculata*, and considerably higher in the triploid hybrids between them, indicating that in this case the differences in the linear order of gene sequences of homologous chromosomes are less within an individual of one species than between individuals of two different species.

This work was done under the supervision of Professor Karl Sax, whom the author wishes to thank for his advice and criticisms.

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FACTOR Z IN HYBRID MAIZE[1]

WILLIAM J. ROBBINS

(WITH THREE FIGURES)

In an earlier paper (3) it was reported that extracts of the partially germinated grains of a hybrid corn had per embryo, per endosperm or per grain a greater growth-promoting effect upon *Phycomyces* in a solution of minerals, sugar, asparagine and thiamin than those of either of the inbred parents. The growth-promoting effect was ascribed to the presence of an unidentified growth substance called, for convenience, factor Z. The present paper reports the results for extracts of grains of another set of inbred maize and the F_1 offspring.

METHODS AND MATERIALS

The grains used were kindly supplied by Dr. Frederick D. Richey. According to Richey *4–8* is an inbred of some 20 years that is used in a number of corn belt hybrids; *187* is also so used and has been selfed for some 14 years. The cross between them (either way) is the seed parent for United States hybrid *44*, which has had an excellent record in Iowa, Illinois, Indiana, and Ohio. The two hybrids were *985*, a cross of *4–8* × *187*, and *995*, a cross of *187* × *4–8*. The grains were of the 1939 crop and the experiments reported here were performed in March and April, 1940.

The growth-promoting properties were determined by extracting the grains with 5 per cent aqueous pyridine. The pyridine extracts were evaporated nearly to dryness and the residue taken up in distilled water. Aliquots of the extracts were added to a solution of minerals, sugar, asparagine, and thiamin and the mycelial growth of *Phycomyces* was determined for a 72-hour period at 25° C.

The basic solution, solution I, contained per liter 50 g. dextrose, 1.5 g. KH_2PO_4, 0.5 g. $MgSO_4 \cdot 7\ H_2O$, 0.5 mg. thiamin, and asparagine as indicated. The following trace elements also were added in p.p.m., 0.005 B, 0.02 Cu, 0.1 Fe, 0.01 Ga, 0.01 Mn, 0.01 Mo, and 0.09 Zn.

Pyrex glass cleaned with chromic acid cleaning mixture and thoroughly rinsed with tap water and distilled water was used throughout. The dextrose was Corn Products Company C.P.; the asparagine was purified by crystallization from alcohol, the thiamin was Merck's synthetic. Other chemicals were of the usual C.P. grade. The plus strain of *Phycomyces Blakesleeanus* was used. Dry weights of the fungus were determined by filtering the mycelium into Gooch crucibles, washing with distilled water and drying at 100° C.

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[1] Assistance in this work was furnished by the personnel of Works Projects Administration Official Project 65–1–97–23 W. P. 5.

EXPERIMENTS

Experiment 1. Twenty grains of each line were placed at 25° C. in a Petri dish with 8 ml. of water. The air-dry weight of each lot of grains was as follows: *4–8*, 4.725 g.; *187*, 5.775 g.; *985*, 4.450 g.; *995*, 4.350 g. After 24 hours each lot of grains was separated into embryos and endosperms. The embryos of each lot were ground in a mortar, as were the endosperms also, and extracted for 24 hours with 50 ml. of 5 per cent aqueous pyridine. The liquid was centrifuged from the solid material and evaporated nearly to dryness on a hot plate. Each extract was made up to 20 ml. with distilled water. One ml. of the final solution was equivalent to the extract of a single embryo or of a single endosperm.

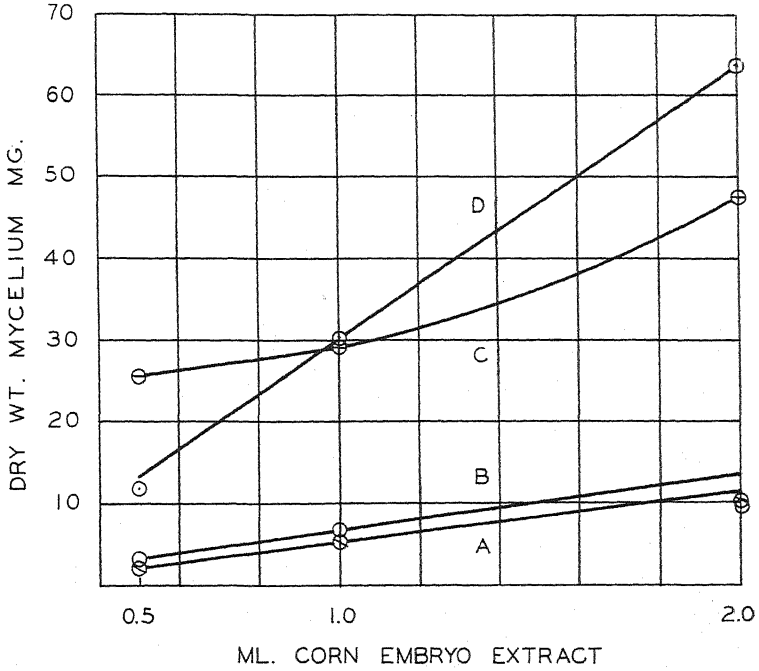

FIG. 1. Increase in dry weight of *Phycomyces* produced by extracts of embryos of maize grains germinated 24 hours. Extracts added to medium of sugar, minerals, asparagine and thiamin. A = line *4–8*, B = line *187*, C = *985*, *4–8* × *187*, D = *995*, *187* × *4–8*. 1 ml. extract = 1 embryo.

The growth-promoting power of each of the 8 extracts was determined by adding aliquots to 25 ml. of solution I containing 2 g. of asparagine per liter. The solutions were inoculated with the spores of *Phycomyces* and incubated at 25° C. The experiment was performed in duplicate. The dry weight of the mycelium produced was determined (table 1) at the end of 72 hours. For constructing the curves in figures 1, 2, and 3 the increase in dry

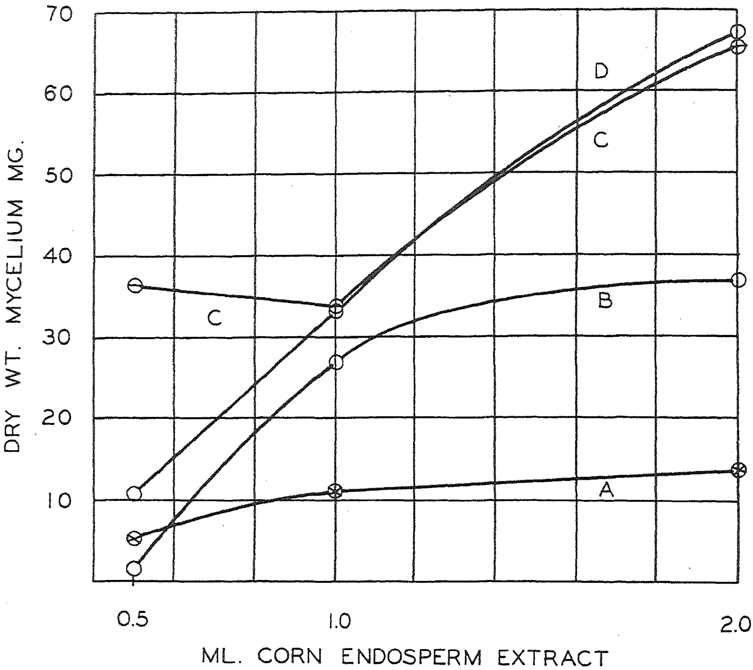

FIG. 2. Increase in dry weight of *Phycomyces* produced by extracts of endosperm of maize grains germinated 24 hours. Extracts added to medium of sugar, minerals, asparagine and thiamin. A = line *4–8*; B = line *187*; C = *985, 4–8* × *187*; D = *995, 187* × *4–8*. 1 ml. extract = 1 endosperm.

TABLE 1

Growth-promoting effect of extracts of embryo and endosperm of inbred maize and their F_1 hybrids upon growth of Phycomyces in a solution of minerals, sugar, asparagine, and thiamin. Grains were germinated for 24 hours.

Quantity of extract added per 25 ml. basic medium	Dry wt. mycelium in 2 flasks mg.			
	4–8	*187*	*985, 4–8 × 187*	*995, 187 × 4–8*
Embryo				
0.5 grain	7.3	8.2	30.7	17.1
1.0 grain	10.4	11.9	34.3	35.4
2.0 grains	15.2	14.8	62.6	68.9
None	5.1	5.1	5.1	5.1
Endosperm				
0.5 grain	10.4	6.7	41.5	15.8
1.0 grain	16.2	32.1	38.7	38.2
2.0 grains	19.0	42.8	70.6	72.3
None	5.1	5.1	5.1	5.1
Net embryo and endosperm				
0.5 grain	7.5	6.7	41.5	15.8
1.0 grain	16.3	32.1	38.7	38.2
2.0 grains	19.0	42.8	70.6	72.3

weight of the mycelium caused by the extracts was used; the dry weight of the mycelium in the solution with no extract was subtracted in each instance from that obtained in the same medium to which the given quantity of extract had been added. All the extracts increased the growth of *Phycomyces* in the presence of thiamin; those of the endosperms were more beneficial than those of the embryos. The difference between the effectiveness of endosperm and embryo extracts was greater for the inbred parents than for the F_1 hybrids (table 1).

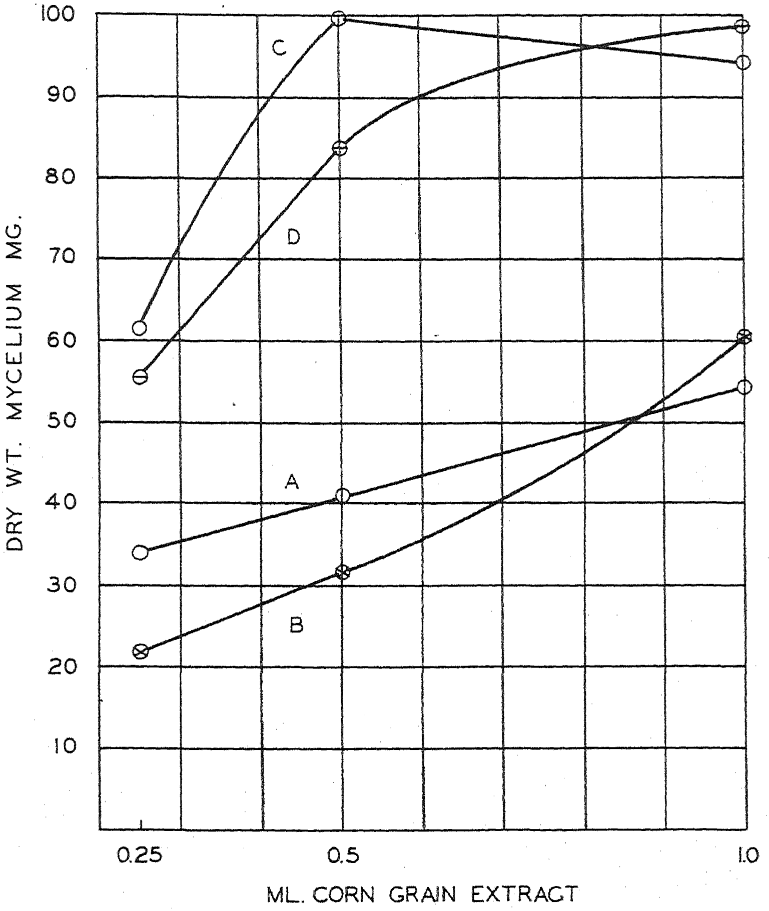

FIG. 3. Increase in dry weight of *Phycomyces* produced by extracts of air dry grains of maize. Extracts added to medium of sugar, minerals, asparagine and thiamin. A = line *4–8*; B = line *187*; C = *985*, *4–8* × *187*; D = *995*, *187* × *4–8*. 1 ml. extract = 1 grain.

It was found earlier (3) that the amount of factor Z increased with the length of the germination period, at least up to 3 days. It was thought desirable to determine whether this increase was associated with the normal germination processes or whether it was accounted for by digestion caused by the enzymes of the grain. This was investigated by comparing the growth promoting properties of extracts of dry grains and of grains which had been permitted to autolyze in the presence of toluene.

Experiment 2. Twenty grains of each line were placed in 125 ml. stoppered Erlenmeyer flasks with 8 ml. of distilled water and 0.5 ml. of toluene. The air dry weights of the several lots of grains were as follows: *4–8*, 4.900 g.; *187*, 5.775 g.; *985*, 4.750 g.; *995*, 4.775 g. After 3 days at about 20° C. the grains had swollen materially and softened. They were removed, ground in a mortar and extracted for 24 hours with 50 ml. of 5 per cent aqueous pyridine.

At the same time another lot of 20 grains of each line was selected. The air dry weights were as follows: *4–8*, 4.925 g.; *187*, 5.875 g.; *985*, 4.700 g.; *995*, 4.875 g. These were crushed and ground without the addition of water or toluene and extracted with 50 ml. of 5 per cent aqueous pyridine.

The liquid from each of the 8 lots of corn grains was separated from the solid material by centrifuging and the extract evaporated on a hot plate nearly to dryness. This removed the pyridine and the toluene. The extract of each lot of grain was made up to 20 ml. with distilled water. One ml. of the final solution was equivalent to the extract of 1 grain.

The effect of the 8 extracts upon the growth of *Phycomyces* in the presence of thiamin was determined. The extract of 1, 0.5, or 0.25 grain was added to 25 ml. of solution I containing 2 g. asparagine per liter. The experiment was performed in duplicate. The flasks were inoculated with the spores of *Phycomyces* and the dry weight of the mycelium was determined after 72 hours incubation at 25° C. (table 2). The dry weights of mycelium

TABLE 2

Growth-promoting effect of extracts of grains of inbred maize and their F_1 hybrids upon growth of Phycomyces in a solution of minerals, sugar, asparagine, and thiamin. Above, extracts of autolyzed grains; below, extracts of dry grains.

Quantity of extract added per 25 ml. basic medium	Net dry wt. mycelium in 2 flasks mg.			
	4–8	*187*	*985*, *4–8 × 187*	*995*, *187 × 4–8*
Autolyzed grains				
1 grain	70.2	75.4	86.1	81.8
0.5 grain	59.9	51.2	60.4	65.6
0.25 grain	33.5	41.7	52.8	52.9
Dry grains				
1 grain	54.1	60.2	94.1	98.9
0.5 grain	40.9	31.5	99.8	83.7
0.25 grain	33.9	21.8	61.5	55.5
None	10.5	10.5	10.5	10.5

grown in the presence of the extracts were expressed as the difference between the weights obtained in solutions with extract and that in solutions with no extract added. For example, the dry weight with the extract of 1 grain of the autolyzed *4–8* line was 80.7 mg.; in the check solution 10.5 mg. of mycelium were obtained; the net dry weight was 70.2 mg.

The extracts of the dry grains of the hybrids were more effective than those of either parent (fig. 3). Autolysis increased the potency of the extracts of the parents but decreased that of the extracts of the hybrids. Since the effects of the extracts of the autolyzed grains were not greater for all 4 lines than those of the grains which were not autolyzed it would seem that the increase in factor Z with germination was not merely caused by enzymatic action but was associated with the normal processes of germination.

The dry weights of mycelium obtained with extracts of the dry grains in experiment 2 were greater than those obtained in experiment 1 with grains germinated for 24 hours. This difference is not believed to be significant, because of the influence of differences in the quantity of inoculum and other factors which can be made uniform for a particular experiment but cannot be controlled from experiment to experiment. Furthermore extracts of whole grains were used in experiment 2 while the embryo and endosperm were separately extracted in experiment 1.

DISCUSSION

The results of these experiments confirm earlier findings (3) with another set of inbred maize and their F_1 heterotic hybrid but leave many questions unanswered.

Will other heterotic maize hybrids resemble those which I have investigated? How would the extracts of non-heterotic maize hybrids influence the growth of *Phycomyces* as compared with those of their inbred parents? There are also instances of "negative heterosis" which might be investigated. I have expressed the results in terms of a single embryo, endosperm, or grain. Would similar results be found per gram of material extracted? Would extracts of the grown plants of maize inbreds and their F_1 hybrids differ in their effects upon *Phycomyces* as those of the grains and seedlings apparently do or are the differences described in this paper and an earlier one limited to the seedling stages only? Would the extracts of heterotic hybrids of plants other than maize affect *Phycomyces* as those of maize do? To what may the beneficial effects of the corn extracts on the development of *Phycomyces* be ascribed? The causes for the favorable action of plant extracts upon *Phycomyces* have been discussed at length elsewhere (1, 2, 4) and it seemed probable that unidentified growth substances, called factor Z, were concerned. Robbins and Hamner (5) presented evidence that factor Z is multiple, consisting of at least two parts, factor Z_1 and factor Z_2. Are both factors concerned in the effects of the corn grain extracts used in this investigation? Is the favorable action due to the addition of organic acids, to changes in hydrogen-ion concentration, to changes in the amount of proportions of minerals, to additions of amino acids, or to some other well known substances rather than unidentified growth substances as we have been inclined to believe?

There are many difficulties in interpreting the effects of plant extracts upon growth because such extracts are mixtures of many organic and inorganic substances, some beneficial, some detrimental, and others ineffective. Until the substances concerned in such an effect as that described in this paper are available in pure form conclusions must be tentative and used primarily as the basis for further experimentation.

SUMMARY

Extracts of the grains of two inbred strains of maize and their heterotic F_1 hybrids were found to increase the early growth of *Phycomyces* in solutions of sugar, minerals, asparagine, and thiamin. The extracts of the hybrid grains produced a greater effect per grain, per embryo, and per endosperm than those of either of the parents. The effect of extracts of autolyzed grains differed somewhat from those which were allowed to germinate for 24 hours.

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THE DEVELOPMENT OF THE EMBRYO SAC IN AGAVE VIRGINICA

LORRAINE REGEN

(WITH FOURTEEN FIGURES)

The vast majority of Angiosperms in which the development of the macrogametophyte has been studied are characterized by an embryo sac of the "normal" type, which is 8-nucleate at maturity, and formed from a single macrospore nucleus in consequence of three nuclear divisions (Maheshwari, 1937). Until recently, *Lilium* has been used as the customary material for the demonstration of embryo sac development to students of elementary botany. It has been shown, however, by Bambacioni (1928, 1932) and Cooper (1934, 1935) that the eight nuclei of the mature embryo sac of *Lilium* are derived from four macrospore nuclei rather than one, and that this 8-nucleate stage is separated from the macrospore nuclei by only two nuclear divisions rather than three. Hence the development of the embryo sac in *Lilium* does not conform to the "normal" type, but is referred to the so-called "Fritillaria" type of Maheshwari (1937).

Several years ago, Dr. Harold C. Bold became interested in attempting to find other favorable material to demonstrate the "normal" type of embryo sac development, and suggested that *Agave virginica* L. (Amaryllidaceae, subfamily Agavoideae) might prove suitable for this purpose. Apparently the only previous cytological work dealing with embryo sac development in this genus is that of Schlimbach (1924), on *Agave chloracantha* and *A. attenuata*, as well as several other representatives of the Amaryllidaceae. This worker concluded that embryo sac development proceeded according to the "normal" type in species whose ovules are surrounded by two integuments, but that development of species with one integument was of the "Lilium" type (as it was understood at that time, now called the "Adoxa" type).

MATERIALS AND METHODS

The inflorescence of *A. virginica* is a panicle or compound raceme, in which many flowers are borne in acropetal succession. It was very easy, therefore, to secure numerous flower buds in all stages of development. The material on which the present study is based was collected by Dr. Harold C. Bold near Knoxville, Tenn., in the summer of 1938, and fixed in a modified Bouin's solution called Allen's B–15.[1] After washing, the material was dehydrated in an alcohol series, cleared in xylol, and, following infiltration, was embedded in paraffin. Sections were cut at a thickness of

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[1] This formula is given by McClung (1929).

10 μ and 15 μ, stained with Heidenhain's iron alum hematoxylin, and counterstained with fast green.

OBSERVATIONS

The flowers of *A. virginica* have an inferior ovary, as is characteristic of the family Amaryllidaceae. In each of the three locules of the ovary are borne two rows of ovules with axile placentation; the ovules themselves are anatropous. Certain cells of the ovary wall are conspicuous because they contain groups of calcium oxalate crystals of the raphides type.

The outer integument of the ovule is from one to three cells thicker than the inner integument, which is usually two cells thick. Within the nucellus, the primary archesporial cell or macrospore mother cell, hypodermal in position, is distinguished from the surrounding cells by its larger size (fig. 1). During the prophases of the heterotypic division the chromatic strands are first evenly distributed throughout the large nucleus, later aggregated in a dense netted mass toward one side. The nucleus generally contains a single large nucleolus, but occasionally there are two nucleoli lying close together. As the chromosomes take definite shape, they become distributed around the periphery of the large prophase nucleus.

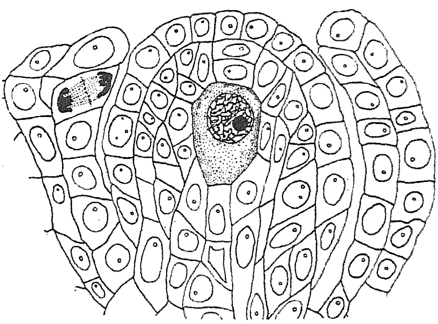
Following the metaphase (fig. 2) and telophase (fig. 3) of the heterotypic division, a cell wall is formed separating the two cells of the dyad (fig. 4). The succeeding homoeotypic division, of which a telophase stage is shown in figure 5, is also followed by wall formation so as to delimit the four macrospores.

The arrangement of the macrospores in the tetrad is either of the linear type (fig. 6) or the "T-shaped" type (fig. 7). In several ovules a row of three reproductive cells was observed with no fourth cell in the adjacent sections; this is possibly to be interpreted as comprising two macrospores and an undivided cell of the dyad.

In every case observed, it is the chalazal macrospore which develops into the embryo sac (fig. 8). The densely staining remnants of the three disintegrating macrospores may be seen at the micropylar end of the enlarging gametophyte as late as the four-nucleate stage (fig. 10).

The nucleus of the chalazal macrospore divides to form a two-nucleate embryo sac (fig. 9). These two daughter nuclei then divide again, forming a four-nucleate macrogametophyte (fig. 10). With the final division of each of these four nuclei, the embryo sac becomes eight-nucleate (fig. 12). At this stage three antipodal cells are formed at the chalazal end of the embryo sac (fig. 11–13), two synergids and an egg cell are formed in the micropylar end (fig. 12–13), and the two polar nuclei migrate toward the center of the embryo sac (fig. 12).

Certain nuclear changes within the embryo sac may occur before fer-



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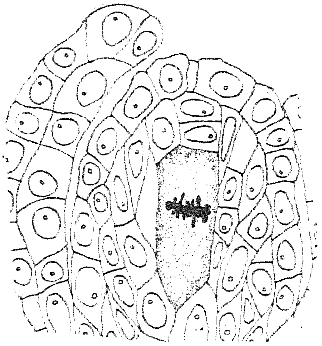

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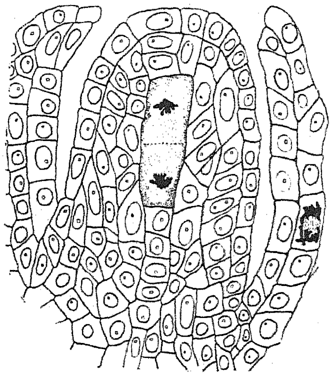

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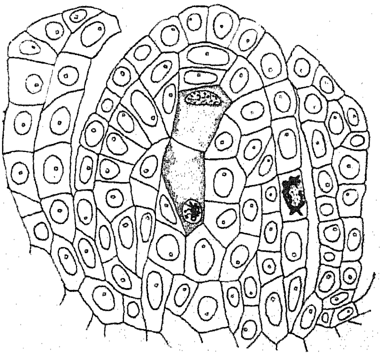

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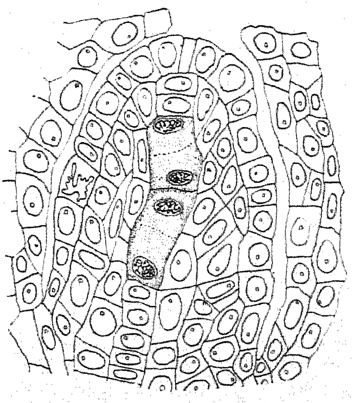

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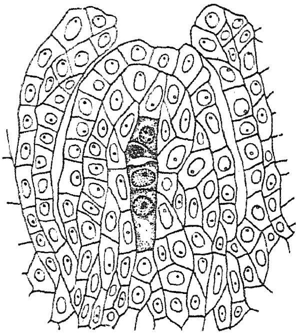
FIG. 1. Early prophase of heterotypic division in the macrospore mother cell. × 320. FIG. 2. Metaphase of heterotypic division. × 340. FIG. 3. Telophase of heterotypic division. × 260. FIG. 4. Dyad formed after heterotypic division. × 340. FIG. 5. Late telophase of homeotypic division. × 300.



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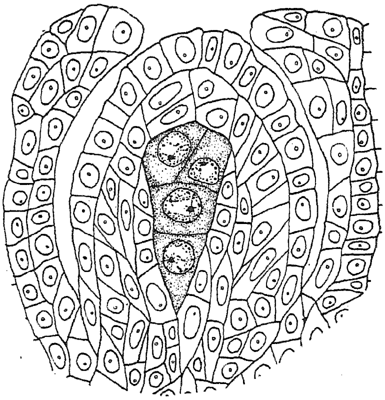

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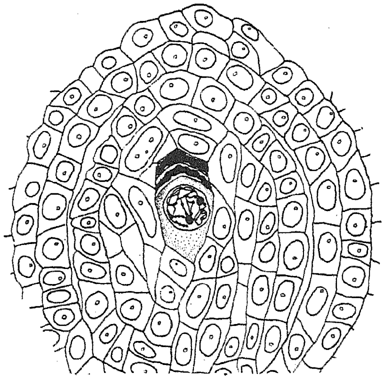

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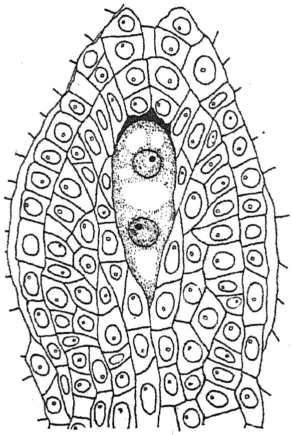

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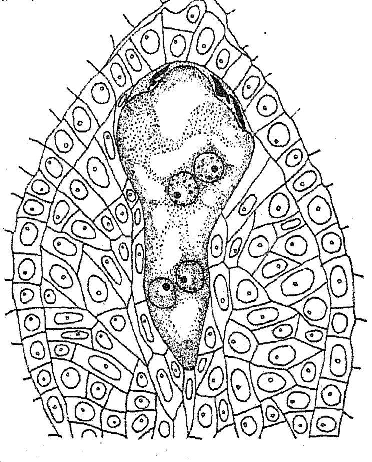

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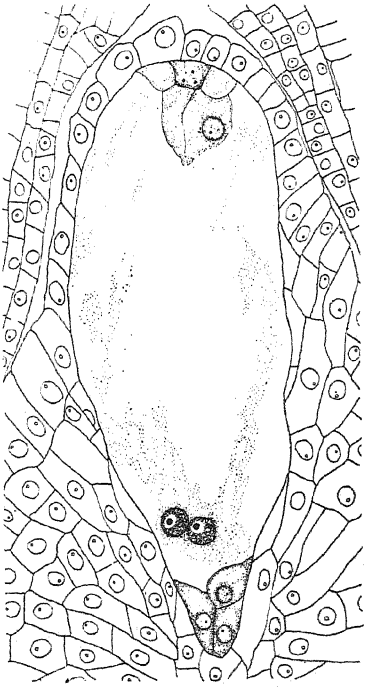
FIG. 6. Tetrad of macrospores showing linear arrangement. ×185. FIG. 7. "T-shaped" tetrad of macrospores. ×340. FIG. 8. Developing chalazal macrospore with two degenerating macrospores. ×250. FIG. 9. Two-nucleate embryo sac. ×200. FIG. 10. Embryo sac at four-nucleate stage, with persistent remnants of three disintegrated macrospores. ×200.



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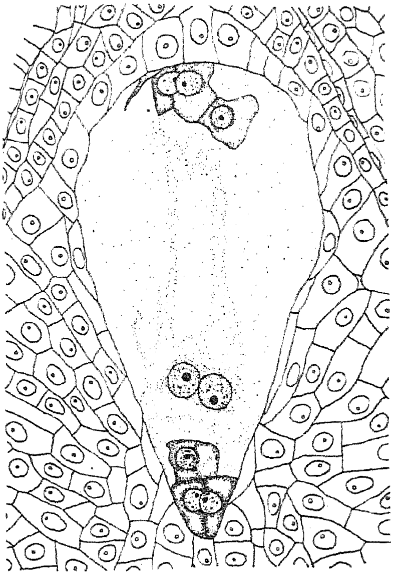

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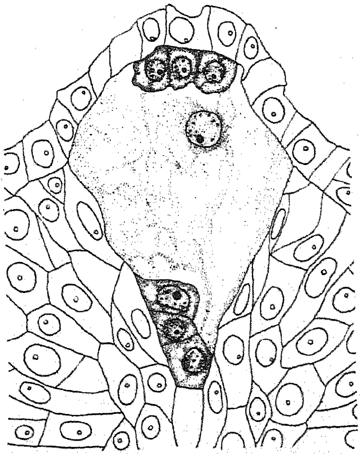

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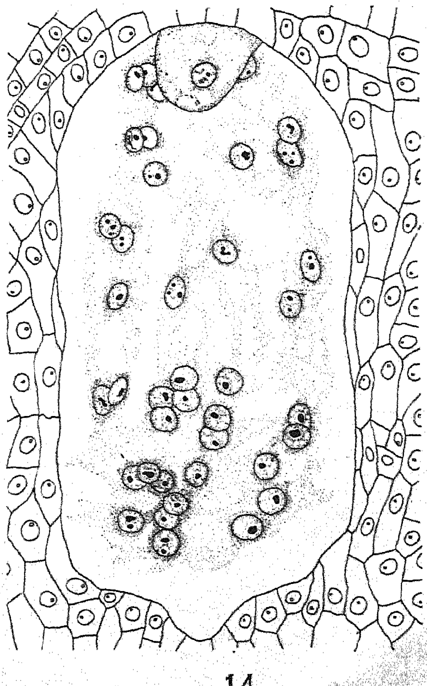

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FIG. 11. Nearly mature embryo sac with egg cell, two degenerating synergids, two

tilization is accomplished. In some cases the synergids (fig. 11) or the antipodals may become disorganized prior to fertilization. The two polar nuclei frequently fuse to form the primary endosperm nucleus, so that the embryo sac is seven-nucleate (fig. 13). This fusion is not of invariable occurrence, however; in certain cases the polar nuclei may remain unfused until after the degeneration of the synergids, of the antipodals, or both.

The actual process of fertilization was not observed in any of the material studied. The most mature ovules examined showed, however, that the endosperm in its early development is free-nuclear (fig. 14). A large number of endosperm nuclei lie in the cavity occupied by the embryo sac before the embryo has begun its development. This observation is in accord with the findings of Schlimbach (1924), who reported a free-nuclear endosperm in *A. chloracantha* and *A. attenuata*.

A number of departures from the normal course of development in *A. virginiana* were observed in the course of the present work. One ovule of this species was found to contain two distinct nucelli, enclosed within the same outer integument, but having separate inner integuments. An account of a similar circumstance has been reported in *Moringa oleifera* of the Liliaceae by Puri (1934). In another ovule, two tetrads of macrospores, each linear in nature, were observed within a single nucellus.

It was noted, furthermore, that a considerable number of ovaries in *A. virginica* were very unproductive. Many of the ovules of such ovaries were sterile and abortive, forming no reproductive cells, and some were actually hollow because of the degeneration of nucellar and sporogenous tissue. Cappelletti (1927), studying deteriorative processes within ovules of *A. chloracantha* in which fertilization was inhibited, described a brief hypertrophy of the nucellar nuclei, followed by cellular degeneration of this tissue and a breakdown of the embryo sac. A similar degeneration occurs in *A. virginica* also; in some cases even after the embryo sac has reached the four-nucleate stage. Likewise Catalano, working with *A. zapupe* (1928) and *A. sisalana* (1929a) noted abnormalities during macrosporogenesis and consequent sterility in these forms, which he would attribute to their probable hybrid nature (1929b).

DISCUSSION

Macrosporogenesis and embryo sac development in *A. virginica* is of the "normal" type, as described by Maheshwari (1937). In this respect, and also in the free-nuclear nature of the young endosperm, *A. virginica* is similar to *A. chloracantha* and *A. attenuata* (Schlimbach 1924). It is hoped that this species may furnish a useful and appropriate material for laboratory illustration of the "normal" type of embryo sac development in the Angiosperms. The occasional abnormalities noted are not of such common occurrence as to preclude its use for this purpose, to which it seems ideally adaptable because of the large size of the nuclei and the embryo sac itself.

McKelvey and Sax (1933) and Whitaker (1934) have suggested that *Agave, Fourcroya, Polyanthes,* and *Beschorneria* of the Amaryllidaceae represent the epigynous counterparts of the hypogynous Liliaceae *Yucca, Hesperoyucca, Hesperaloe, Cleistoyucca,* and *Samuela.* This suggestion is based on the fact that all of these genera have an identical haploid chromosome complement consisting of five large and twenty-five small chromosomes. The present work, showing that *Agave* is like *Yucca* (Wolf 1940, et al.) in having a "normal" type of embryo sac, would tend to strengthen this point of view.

SUMMARY

In *Agave virginica* L. the macrospore mother cell forms four macrospores, which may have either a linear or a "T-shaped" arrangement. The chalazal macrospore, by three nuclear divisions, forms an embryo sac of the "normal" eight-nucleate type, which becomes seven-nucleate following the fusion of the two polar nuclei to form the primary endosperm nucleus. Both the synergids and the antipodals may degenerate before fertilization. Endosperm formation is free-nuclear, and may proceed to a considerable extent before development of the embryo has begun. Degeneration of the embryo sac and nucellus in unfertilized ovules has been observed.

The author wishes to express her sincere thanks to Dr. Harold C. Bold for suggesting the problem and supervising the early stages of this work, and to Dr. Fred T. Wolf for his assistance in the preparation of the drawings and the manuscript.

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SUPPLEMENTARY NOTES ON AMERICAN MENISPERMACEAE

B. A. Krukoff and H. N. Moldenke

Considerable progress has been made recently in the chemical studies of the alkaloids derived from certain members of the *Menispermaceae* (3) and in the studies of botanical components of various Curare (1, 2, 6, 7). In connection with this continuous interest in Curare, a number of menispermaceous specimens have been received for identification which extend our knowledge of certain species. Extensions of ranges are noted for a number of species and one species is described as new. It is satisfactory that, although a considerable number of specimens has been examined, no changes in nomenclature appear to be necessary at the present time.

The species are arranged in the same order and the place of deposit of specimens is shown by the same abbreviations as in our previous papers (4, 5). The following new abbreviations are used:

A: Arnold Arboretum, Harvard University.
D: Academy of Natural Sciences, Philadelphia.
E: Missouri Botanical Garden, St. Louis.
Mi: University of Michigan, Ann Arbor.

CHONDODENDRON Ruíz & Pavon

1. CHONDODENDRON MICROPHYLLUM (Eichl.) Moldenke. Additional specimens examined: BRAZIL—BAHIA: *Blanchet 1594* (F), *3178a* (F), *s.n.* (F).

2. CHONDODENDRON PLATIPHYLLUM (A. St. Hil.) Miers. Additional specimens examined: BRAZIL—RIO DE JANEIRO: *St. Hilaire s.n.* (Macbride photo 34501; type coll. of *Cocculus ? cinerascens*) (F—photo). STATE UNDETERMINED: *Martius 510* (Macbride photo 19125; type coll. of *C. aemulum*) (E, F, G—photo). BAHIA: *Luschnath* or *Lhotsky 173* (E).

In his recent paper (3, p. 737) dealing with the alkaloids of *Chondodendron* spp. Dr. King states: "The aim of this investigation was the determination of the botanical source of the substance known in pharmacy as *radix pareirae bravae*, since its alkaloids are related to the phenolic alkaloids of tube- and pot-curare. This object has been attained. When *pareira brava* yields l-bebeerine it comes from *Chondodendron platyphyllum* and when it yields d-bebeerine from *Ch. microphyllum.*" In another place in the same paper (3, p. 739) he states: "*Chondodendron platyphyllum* and *microphyllum* are two species whose taxonomical characters are very close, but chemical examination shows a clear distinction. Since it is unlikely that native plant collectors could distinguish these species and there is no apparent difference in the pharmacognostical characters of their roots, it seems clear that *pareira brava* has originated in the past in these two species."

It is thus satisfactory that our suggestion in a previous paper (4, p. 15) as to the botanical source of "pareira brava" has been fully confirmed.

3. Chondodendron tomentosum Ruíz & Pav. Additional specimens examined: Peru—san martín: basin of Río Huallaga, *Klug 4044* (E, F, G, W); *Spruce 4474* (Macbride photo 34500; type coll. of *C. cretosum* and *Botryopsis Spruceana*) (F, F—photo, G). junín: basin of Río Perene, *Killip & Smith 27175* (F).

5. Chondodendron limaciifolium (Diels) Moldenke. Additional specimens examined: Brazil—amazonas: basin of Rio Solimoes, *Krukoff 8370* (W), *8522* (W), *8713* (W). pará: *Sigueira 8266* (Macbride photo 4993) (G—photo of type).

6. Chondodendron tomentocarpum (Rusby) Moldenke. Additional specimens examined: Bolivia—la paz: basin of Río Beni, *O. E. White 1812* (type coll. of *Abuta boliviana*) (G, Mi, W).

7. Chondodendron toxicoferum (Wedd.) Krukoff & Moldenke. Additional specimens examined: Peru—loreto: basin of Río Huallaga, *Killip & Smith 28665* (F); *Klug 2782* (E, F, G); basin of Río Itaya, *Killip & Smith 29337* (F); basin of Río Putumayo, *Klug 2042* (E, F, G, Mi). Brazil: basin of Rio Jurua, *Ule 5631* (Macbride photo 4985; type coll. of *C. polyanthum*) (F, G—photo).

SCIADOTENIA Miers

1. Sciadotenia Sagotiana (Eichl.) Diels. Additional specimens examined: French Guiana: *Sagot 19* (Macbride photo 4987) (G—photo of type).

2. Sciadotenia paraënsis (Eichl.) Diels. Additional specimens examined: Brazil—pará: *Martius s.n.* (Macbride photo 19124) (G—photo of type).

3. Sciadotenia solimoesana Moldenke. Additional specimens examined: Brazil—amazonas: basin of Rio Solimoes, *Krukoff 8243* (A), *8385* (A—isotype).

4. Sciadotenia Eichleriana Moldenke. Additional specimens examined: Brazil—amazonas: basin of Rio Solimoes, *Krukoff 8279* (A—isotype, W—isotype), *8376* (A).

6. Sciadotenia ramiflora Eichl. Additional specimens examined: Peru—loreto: basin of Río Huallaga, *Poeppig 2271* (Macbride photo 4986) (G—photo of type); basin of Río Amazonas, *Klug 1299* (W).

7. Sciadotenia Duckei Moldenke. Additional specimens examined: Brazil—amazonas: *Ducke 409* (A—isotype, F—isotype).

8. Sciadotenia amazonica Eichl. Additional specimens examined: Brazil—amazonas: *Martius s.n.* (Macbride photo 19126) (G—photo of type).

9. Sciadotenia cayennensis Benth. Additional specimens examined: French Guiana: *Collector undesignated s.n.* (F). British Guiana—essequibo: basin of Takutu River, *A. C. Smith 3581* (E).

Dr. Smith gives the following notes: "Slender liana; fruit often on stem near base, the leaves above; fruit orange, at length deep purple." The collection is the first known record of the species from British Guiana.

10. Sciadotenia brachypoda Diels. Additional specimens examined: Brazil—Amazonas: basin of Rio Jurua, *Krukoff 5096* (A, Mi, W); basin of Rio Purus, *Goeldi 3934* (Macbride photo 4984) (G—photo of isotype).

11. Sciadotenia similis Moldenke. Additional specimens examined: Brazil—Amazonas: basin of Rio Negro, *Krukoff 8020* (A—isotype).

ANOMOSPERMUM Miers

1. Anomospermum Schomburgkii Miers. Additional specimens examined: Peru—San Martín: basin of Río Huallaga, *Klug 3739* (A, E, F, G, W), *3756* (E, F, G). Huanuco: *Mexia 8201* (E, G, W). Loreto: basin of Río Nanay, *Klug 1191* (W), *1370* (F, W). Bolivia—La Paz: basin of Río Beni, *Buchtien 1619* (G). Brazil: Amazonas: basin of Rio Negro, *Spruce 2563* (Macbride photo 34503; type coll. of *A. lucidum*) (F, F—photo, G). Rio de Janeiro: *Glaziou 13516* (Macbride photo 4997) (A, F, G—photo). Surinam: *Hostmann 1298* (Macbride photo 30147; type coll. of *A. Hostmanni*) (F—photo, G). British Guiana: *Rob. Schomburgk 833* (Macbride photo 30148) (F—isotype, F—isotype, F—photo of isotype, W—isotype). Demerara: basin of Demerara River, *De la Cruz 2682* (D, G, W). Essequibo: basin of Essequibo River, *De la Cruz 1436* (D, E, W), *1732* (E, W); basin of Mazaruni River, *De la Cruz 2267* (D, E, Mi, W), *2285* (D, E, W), *2360* (E, W), *2835* (D, E, G, W). Trinidad: *W. E. Broadway 7552* (W).

The Mexia collection cited above represents the first known record of this species from Huanuco. The collector records the vernacular name ''huano'' and states that the mature fruit is orange. The New York Botanical Garden sheet of *Buchtien 619* is plainly so labeled, but the Gray herbarium sheet has had the number corrected to ''1619.'' The reason for this correction is not clear. The Broadway collection cited above is apparently the first record of the species from Trinidad.

2. Anomospermum Dielsianum Moldenke. Additional specimens examined: Brazil—Amazonas: basin of Rio Solimoes, *Krukoff 9045* (A—isotype).

3. Anomospermum reticulatum (Mart.) Eichl. Additional specimens examined: Brazil—Amazonas: basin of Rio Japura, *Martius 3027* (Macbride photo 19128) (G—photo of cotype); basin of Rio Madeira, *Krukoff 6766* (A).

4. Anomospermum nitidum Miers. Additional specimens examined: Brazil—Rio de Janeiro: *Miers 4254* (F—isotype); *Glaziou 13517* (F).

6. Anomospermum chloranthum Diels. Additional specimens examined: Brazil—Amazonas and Acre Territory: basin of Rio Purus, *Ule 9388* (Macbride photo 4996) (F—isotype, G—photo of type); basin of Rio Solimoes, *Krukoff 9118* (A).

TELITOXICUM Moldenke

1. Telitoxicum Krukovii Moldenke. Additional specimens examined: Brazil—Amazonas: basin of Rio Madeira, *Krukoff 6912* (A—isotype).

2. Telitoxicum peruvianum Moldenke. Additional specimens examined: Peru—Loreto: basin of Río Putumayo, *Klug 2129* (E—isotype).

5. Telitoxicum Duckei (Diels) Moldenke. Additional specimens exam-

ined: BRAZIL—PARÁ: basin of Rio Mapuera, *Ducke 9012* (Macbride photo 4990) (G—photo of type).

6. TELITOXICUM MINUTIFLORUM (Diels) Moldenke. Additional specimens examined: PERU—LORETO: basin of Río Marañon, *Tessmann 4565* (F—isotype). BRAZIL—AMAZONAS: basin of Rio Solimoes, *Krukoff 7559* (A), *8840* (A, W); basin of Rio Negro, *Krukoff 7956* (A), *8033* (A).

ABUTA Barrère

1. ABUTA MACROCARPA Moldenke. Additional specimens examined: BRAZIL—AMAZONAS: basin of Rio Negro, ? *Krukoff 7961* (A), ? *7994* (A).

2. ABUTA OBOVATA Diels. Additional specimens examined: BRITISH GUIANA—ESSEQUIBO: basin of Mazaruni River, *De la Cruz 2250* (D—isotype, E—isotype, G—isotype, W—isotype).

3. ABUTA BULLATA Moldenke. Additional specimens examined: BRAZIL—AMAZONAS: basin of Rio Madeira, *Krukoff 7051* (A). BRITISH GUIANA—ESSEQUIBO: basin of Potaro River, *Gleason 727* (W).

5. ABUTA VELUTINA Gleason. Additional specimens examined: VENEZUELA—AMAZONAS: basin of Río Orinoco, *Tate 959* (W—isotype).

6. ABUTA PANURENSIS Eichl. Additional specimens examined: BRAZIL—AMAZONAS: basin of Rio Negro, *Spruce 2763* (Macbride photo 4994) (G—photo of isotype).

7. ABUTA RACEMOSA (Thunb.) Triana & Planch. Additional specimens examined: COLOMBIA: department undesignated, *Mutis 5632* (W), *5759* (W).

8. ABUTA IMENE (Mart.) Eichl. Additional specimens examined: BRAZIL—AMAZONAS: basin of Rio Negro, *Spruce s.n.* (in vicinibus Barra; Macbride photo 4992; type coll. of *A. rigida*) (F, G, G—photo).

10. ABUTA TRINERVIS (Rusby) Moldenke. Additional specimens examined: BOLIVIA—LA PAZ: basin of Río Mapiri, *Buchtien 1935* (W—isotype).

11. ABUTA GRANDIFOLIA (Mart.) Sandw. Additional specimens examined: VENEZUELA—BOLÍVAR: *Ll. Williams 11437* (F, F, W). PERU—SAN MARTÍN: basin of Río Huallaga, *Klug 2757* (A, E, G). LORETO: basin of Río Huallaga, *Klug 3006* (A, E, G); basin of Río Amazonas, *Klug 2526* (A, W). COLOMBIA—PUTUMAYO: *Klug 1962* (A, E, G). VAUPÉS: *Cuatrecasas 6931* (W). BOLIVIA—LA PAZ: basin of Río Beni, *H. H. Rusby 1979* (D, E, G, Mi). BRAZIL—GOYAZ: *Froes 2065* (A, Mi). MATTO GROSSO: *Malme 1484* (G). MARANHÃO: *Froes 11829* (N). ACRE TERRITORY: basin of Río Purus, *Krukoff 5786* (A, W). AMAZONAS: basin of Rio Jurua, *Krukoff 4720* (A, Mi); basin of Rio Madeira, *H. H. Rusby 1980* (Mi); basin of Rio Solimoes, *Poeppig 3069* (type coll. of *A. concolor*) (F); *Krukoff 7812* (A); basin of Rio Negro, *Spruce 1829* (cotype coll. of *Anelasma pallidum*) (G), *s.n.* ("in vicinibus Barra") (G); *Krukoff 7998* (A). PARÁ: *Ducke 275* (A, F). BRITISH GUIANA—ESSEQUIBO: basin of Takutu River, *Rich. Schomburgk 440* (Macbride photo 30152; type coll. of *Anelasma Guianense* (F, F—photo). BERBICE: basin of Berbice River, *De la Cruz 1646* (E). SURINAM: *Collector undesignated s.n.* ("D," 23–VII–1939) (N).

Cuatrecasas' specimen is the first known record of the species for the province of Vaupés (Colombia), Froes' specimen the first record from the State of Maranhão (Brazil).

The vernacular name "oeralime" is recorded on the label of the specimen from Surinam.

12. ABUTA KLUGII Moldenke. Additional specimens examined: BRAZIL—AMAZONAS: basin of Rio Madeira, ? *Krukoff 7185* (A, E).

13. ABUTA SELLOANA Eichl. Additional specimens examined: BRAZIL: *Sellow s.n.* (D). SÃO PAULO: *F. C. Hoehne s.n.* (Herb. Inst. Biol. S. Paulo 28429) (A). RIO DE JANEIRO: *Glaziou 13403* (F). MINAS GERAES: *Mexia 4456* (A, D, E, G), *5082* (A, D, E, G); *Mello Barreto 1662* (N), *1777* (F), *1950* (F).

14. ABUTA RUFESCENS Aubl. Additional specimens examined: BRAZIL: *Casaretto 1855* (F). RIO DE JANEIRO: *Guillemin 639* (type coll. of *Cocculus ? macrophylla*) (F); *Martius 306* (Macbride photo 19129) (G—photo). MINAS GERAES: *Mexia 4215* (G), *5478* (A, A, D, E, E, G). AMAZONAS: basin of Rio Madeira, *Krukoff 5978* (A, Mi, W); basin of Rio Purus, *Krukoff 5437* (A, E, Mi, W).

16. ABUTA GRISEBACHII Triana & Planch. Additional specimens examined: BRAZIL—AMAZONAS: basin of Rio Solimoes, *Krukoff 7570* (A), *7572* (W), *7822* (A), *8660* (A); basin of Rio Negro, *Krukoff 7960* (A), *7976* (A), ? *8030* (A); *Ducke 415* (A, F); *Spruce 2340* (Macbride photo 4991) (F—cotype, G—cotype, G—photo of cotype).

17. ABUTA CANDOLLEI Triana & Planch. Additional specimens examined: BRITISH GUIANA: basin of Mazaruni River, *Tutin 188* (W). SURINAM: *Collector undesignated s.n.* ("E," 16.VII.1939) (N). FRENCH GUIANA: *Sagot s.n.* (Macbride photo 34498) (F—photo of type); *Perottet s.n.* (F); *Aublet s.n.* (Macbride photo 34499) (F, F—photo).

If the Paris specimen of *Aublet s.n.* (of which we have seen a fragment and a photograph in the Field Museum herbarium) proves to be conspecific with the British Museum specimen which is the type of *A. rufescens* Aubl., then *A. rufescens* will have to be the name adopted for what is now called *A. Candollei*, and the plant now known as *A. rufescens* will have to have a new name.

Tutin's collection is the first record of the species from British Guiana.

18. **Abuta splendida** Krukoff & Moldenke, sp. nov. Frutex scandens; laminis coriaceis ovatis vel late ellipticis, ad apicem abrupte breviterque mucronatis, ad basim rotundatis, supra nitidis, subtus dense adpresso-tomentosis, 5-plinerviis; drupis magnis 2.8–3.1 cm. longis, 1.8–2 cm. latis, asymmetricis.

In our previous paper (5, p. 70) the Buchtien specimens cited below were placed under *A. Candollei* with reservations. They exhibit only pistillate flowers and mature fruits, neither of which was available on any of the specimens from the Guianas which are undoubtedly the true *A. Candollei*. Since then we have received an excellent sheet with mature fruit (*collector undesignated s.n.*) collected on July 16, 1939, at Litanie, in Surinam, and kindly sent to us by Prof. Dr. G. Stahel, also additional sheets of the Bolivian plant collected by the senior author of this paper in 1939 in the basins of the Río Bopi and Río Mapiri.

It is now obvious that the Bolivian plant represents a distinct species. Its fruits are 2.8–3.1 cm. long, 1.8–2 cm. wide, distinctly asymmetric at the base, curved, the mesocarp hard, about 2 mm. thick, and the pedicels 2–3.5 mm. in diameter, whereas in *A. Candollei* the fruits are 1.7–2.1 cm. long, 1.3–1.5 cm. wide, more or less symmetric at the base, and straight, the mesocarp about 0.5 mm. thick, and the pedicels up to 1 mm. in diameter.

Only staminate flowers are known from *A. Candollei* and only pistillate flowers are known from the new species from Bolivia. In our previous paper (4, p. 70) we have already pointed out the differences in the pistillate flowers between the Bolivian plant and *A. Grisebachii*, the only other species of the genus in which the leaf-blades are woolly beneath (completely covered with hairs!). The pistillate flowers of the new species differ from those of *A. Grisebachii* in their much longer and wider sepals, which are distinctly appressed-pubescent with short antrorse buff hairs which project conspicuously in ciliate fashion over the margins, longer staminodes, and larger ovaries.

Description: A woody vine; older branchlets stout, solid, subappressed-tomentose, the pubescence wearing off with age; younger branchlets stout, very densely appressed-tomentose with brownish or cinereous hairs; petioles slender, 2.5–9.5 cm. long, densely subappressed-tomentose with cinereous hairs when young, less so in age, curved and incrassate at apex, ampliate at base; leaf-blades coriaceous, ovate or broadly elliptic, 8–20.5 cm. long, 4.9–13 cm. wide, from rounded to acuminate and invariably abruptly short-mucronate at apex, entire, rounded at base, glabrous above except for the midrib and primary veins near the base which are often subappressed-tomentose with cinereous hairs, densely appressed-tomentose with cinereous hairs below, 5-plinerved, the primary veins and their branches somewhat impressed above, very prominent beneath, the inner pair of primary veins issuing at the very base of the blade; secondaries rather numerous, issuing at approximately right angles to the primaries, subparallel to each other, regular, distinct or often indistinct under a hand-lens above, very prominent beneath; veinlet reticulation fine and abundant, hardly distinct under a hand-lens above, prominent beneath; rachis subappressed-tomentose, the pubescence wearing off with age, greatly incrassate in fruit; fruiting-pedicels stout, 4–9 mm. long, 2–3.5 mm. in diameter, pubescent like the rachis, each bearing 1, 2, or 3 fruits; torus very greatly enlarged and club-shaped in fruit; fruits drupaceous, basally attached, elliptic, 2.8–3.1 cm. long, 1.8–2 cm. wide, asymmetric at the base, curved, the exocarp hard, densely subappressed-tomentose with cinereous hairs, the pubescence wearing off with age, the mesocarp dark-brown, hard, about 2 mm. thick, the endocarp bony, sculptured; embryo folded over the condyle, each arm about 1.6 cm. long.

Specimens examined: BOLIVIA—LA PAZ: basin of Río Bopi, *Krukoff 10652* (N); basin of Río Mapiri, *Krukoff 10802* (N), *10866* (N), *10927* (N), *11083* (fr. Oct.–Nov.) (N—type); *Buchtien 620* (fr. Sept.), (N, G), *1676* (fl. June) (W), *1901* (fr. Sept.) (N, W, W).

The species is very common on a hill on the right bank of the Río Bopi near Malpaso del Cinco, also near Florida (between Mapiri and San Carlos) in the basin of the Río Mapiri. The New York Botanical Garden specimen *Buchtien 620* is plainly inscribed "620," while the Gray herbarium specimen has had its number corrected to "1620." The reason for this correction is not clear.

ELISSARRHENA Miers

1. ELISSARRHENA GRANDIFOLIA (Eichl.) Diels. Additional specimens examined: BRAZIL—AMAZONAS: basin of Rio Jurua, *Krukoff 4673* (A, F); basin of Rio Negro, *Spruce 1538* (Macbride photo 19130) (G—photo of type).

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NEW YORK, NEW YORK

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NOVELTIES IN THE MELASTOMACEAE

H. A. GLEASON

Among the specimens referred to me for identification during the past twelve months are several apparently new to science. These are here described. All types have been deposited in the Britton Herbarium at the New York Botanical Garden.

Weberbauer collected in 1904 a Peruvian melastome which was described by Cogniaux in 1908 as the only species in a new genus, *Centradeniastrum*. So far as I know, it has not been re-collected. Cuatrecasas and Arbeláez have recently collected a second species in Colombia.

Centradeniastrum album Gleason, sp. nov. A *C. roseo* differt floribus 5-meris ovario 3-loculari foliis late cordato-ovatis.

Stem slender, freely branched, glabrous, about 5 dm. long. Petioles slender, glabrous, nearly as long as the blade. Leaf-blades firm, cordate-ovate, 5–20 mm. long, 5–15 mm. wide, subacuminate to a blunt tip, shallowly serrate with 6–9 teeth on each side, 5–7 nerved, glabrous, or with a few short setae above. Cymes to 7-flowered, the nodes subtended by ovate (lower) to lanceolate (upper) bracts 2–3 mm. long; pedicels 5–15 mm. long, glandular-hirsute. Flowers 5-merous. Hypanthium cup-shaped, 3.4 mm. long, thin-walled, 10-ribbed, glandular-hirsute. Sepals reflexed at anthesis, triangular, subulate-tipped, 2.7 mm. long. Petals elliptic, white, 11 mm. long, 7.5 mm. wide, obtuse, tipped with a stout glandular seta. Stamens dimorphic; episepalous series: filaments slender, 5.2 mm. long; thecae nearly straight, subulate, 3.5 mm. long; connective forming a half-circle, prolonged 2.1 mm. to the filament and bearing a short basal dorsal spur, prolonged below the filament 2 mm. in an unlobed flattened organ; epipetalous series: filaments 5.8 mm. long; anthers erect, straight, linear-subulate, 3.5 mm. long; connective not prolonged. Ovary 3-celled; style declined, 7.5 mm. long; stigma punctiform. Seeds flat, cuneate, 1.7 mm. long, wing-margined around the elliptic embryo.

TYPE: *Cuatrecasas & Arbeláez 6239*, from Cerro de Munchique, western Cordillera, Dept. Cauca, Colombia.

Monochaetum calvescens Gleason, sp. nov. Sect. *Bonplandiae*. A *M. Bonplandii* differt ramis petiolis foliis pedicellis brevissime strigosis non patulo-pubescentibus, hypanthio subduplo majore glabro, sepalis minutissime ciliatis ceterum glabris, appendice staminum minorum elliptica.

Younger stems, petioles, leaf-blades and pedicels short-strigose. Petioles slender, 4–8 mm. long. Blades ovate-oblong, up to 35 by 15 mm., short-acuminate, ciliate with ascending hairs, rounded at base, sub-5-pli-nerved, thinly strigose on both sides, glabrous above over the primary veins. Flowers 4-merous, in small clusters terminating the stem and branches, on strigose pedicels 5–10 mm. long. Hypanthium narrowly campanulate, purple-red, glabrous, about 9 mm. long. Sepals triangular-lanceolate, reflexed at anthesis, 9 mm. long, 3–3.5 mm. wide at base, acuminate, minutely ciliate, with a few short setae at the sinus, otherwise glabrous. Petals red-violet, apparently about 15 mm. long. Episepalous stamens: filaments flat, thin, 8.4 mm. long; anthers erect or nearly so, linear-subulate, sterile, 2.2–3.1 mm. long; appendage divergent, flattened, narrowly elliptic, 1.2–1.5 mm. long. Epipetalous stamens: filaments stouter, 7.7–8.3 mm. long; anthers deflexed, linear-subulate, slightly arcuate, opening by a dorso-terminal pore, the thecae 9–10 mm. long; connective 0.5 mm. long, channeled on the ventral side; appendage curved forward into a quarter-circle, 2.5 mm. long, the basal half channeled on the concave side, the distal half flattened, widened, and irregularly 3-lobed. Ovary setose at the summit; style slender, 14 mm. long; stigma punctiform.

TYPE: *Arbeláez & Cuatrecasas 6611*, from Fusagasugá, Dept. Cundimarca, Colombia, alt. 2100–2400 m.

The structure of the stamens places the species beside the well-known *M. Bonplandii* (Kunth) Naud., the only other member of the species-group. The very apparent differences between the two are stated in the diagnosis.

Meriania colombiana Gleason, sp. nov. Sect. *Umbellatae*. Frutex scandens; a *M. quintuplinervi* differt dentibus calycis exterioribus sepala multo excedentibus, a *M. boliviensi* foliis subtus densius tomentosis antheris multo longioribus, a *M. Weberbaueri* structura antherarum et connectivi.

Climbing shrub. Pubescence of spreading hairs densely plumose or stellate at the base only. Younger branches obscurely 4-angled, ferruginous-hirsute, more densely so at the nodes, soon glabrescent. Petioles slender, 2–4 cm. long, hirsute. Blades thin, elliptic, 12–20 cm. long, 5.5–9 cm. wide, acute, essentially entire, rounded at base, 5-pli-nerved, above ferruginous-pubescent when young, soon glabrescent, beneath permanently whitened with hairs up to 2 mm. long, the basal branches 0.4 mm. long. Inflorescence 2 dm. long, pubescent like the stem, the flowers in sessile or stalked clusters of 3, the latter usually with a single flower from the base of the stalk; pedicels 15–20 mm. long. Hypanthium campanulate, thick-walled, 8.5 mm. long to the torus, densely ferrugious-pubescent, the hairs curved-ascending. Calyx-tube prolonged 4.5 mm. to acute sinuses; sepals broadly round-ovate, 2 mm. long, short-acuminate; exterior teeth terete, 6 mm. long, surpassing the sepal by 3 mm. Petals triangular-obovate, 23 mm. long, almost as wide, barely retuse, entire. Stamens nearly isomorphic; filaments stout, flattened, glabrous, 8.4–10.3 mm. long, part of them twisted to bring the anthers parallel with each other; anthers subulate, tangentially flattened, about 8.5 and 10 mm. long, opening by a single pore; connective not elevated, prolonged straight back 1–1.4 mm. as a triquetrous organ (large stamens) or as a nearly terete organ channeled on the dorsal side, bearing at base an erect spur, flat, triangular, 0.7 mm. long in the small stamens, conic and 1 mm. long in the large. Ovary superior, 5-celled; style glabrous, slightly sigmoid, 29 mm. long; stigma truncate.

TYPE: *Arbeláez and Cuatrecasas 5285*, from Dintel, Dept. Cundimarca, Colombia, alt. 2300–2700 m.

M. colombiana, M. quintuplinervis Naud., *M. boliviensis* Cogn., and *M. Weberbaueri* Cogn. form a group of closely related species characterized by large sepals and the peculiar type of pubescence described above. In the second the exterior teeth scarcely extend beyond the sepals, in the third the flowers are much smaller and pubescence sparse, and in the last the connective is elevated into a prominent dorsal ridge and not prolonged at base. *M. umbellata* Karst., which was also assigned to this group by Cogniaux, is quite a different plant, more closely related to the well-known *M. speciosa.*

Diolena purpurea Gleason, sp. nov. Herba humilis cauli hirsuto; folia majora lanceolata brevissime petiolata, minora sessilia reniformia; racemus brevis, floribus confertis 5-meris; hypanthium purpureo-hirsutum; stamina dimorpha, antheris oblongis, connectivo setis 2 ornato, in ser. int. gracilibus 0.6 mm. longis, in ser. ext. 2 mm. longis apice clavatis.

A low herb, the stems hirsute with usually reflexed hairs. Larger leaf-blades lanceolate, 6–12 cm. long, 2–3.5 cm. wide, obtusely acuminate, minutely denticulate, long-ciliate, inequilateral at base, 3-pli-nerved, pilose above, especially on the veins, purple and hirsute beneath. Smaller leaves sessile, reniform, up to 1 cm. long. Raceme short, with crowded, 5-merous, short-pediceled flowers. Hypanthium hemispheric, 2.2 mm. long, densely hirsute with purple hairs. Sepals scarious, truncate-triangular, erose-fimbriate, 0.4 mm. long; exterior teeth subulate, erect, 1.5 mm. long. Petals oblong, 6 mm. long, white, subacute. Stamens dimorphic; filaments slender but flat, 2.1 or 1.5 mm. long; anthers semi-ovoid, nearly 1 mm. long, opening by a ventro-terminal pore; connective prolonged at right angles to the thecae, 0.4 or 0.3 mm. long, bearing two anterior appendages 1.9 mm. long and clavate distally or 0.6 mm. long and slender. Style bent laterally near the apex, 3.6 mm. long, thickened above to the truncate stigma.

TYPE: Killip 35243, from dense forest on the upper Río San Juan, Corcovado Region, Intendencia El Chocó, Colombia, alt. 200–275 m.

It is nearest to *D. auriculata* Triana, from which it differs in its strongly hirsute stem, foliage and hypanthium.

Leandra hylophila Gleason, sp. nov. Rami petioli et panicula strigosa; folia breviter petiolata anguste oblonga utrinque angustata 5-pli-nervia supra strigulosa subtus pubescentia; panicula multiflora pyramidalis; hypanthium subglobosum strigosum; calycis lobi breves triangulares quam dentes exteriores duplo breviores; petala anguste oblonga; ovarium glabrum 3-loculare.

Shrub about 5 m. high, the younger branches roundly 4-angled, closely strigose with brown hairs less than 1 mm. long; petioles stout, 1–2 cm. long, strigose like the stem; leaf-blades thin, narrowly obovate-oblong to oblong-lanceolate, up to 20 by 7 cm., acute or short-acuminate, obscurely denticulate and ciliate, acute or cuneate at base, minutely strigose above (hairs 0.5 mm. long), pubescent beneath with hairs up to 1 mm. long. Panicle short-peduncled, 10 cm. long, freely branched, pubescent like the stem. Flowers sessile, 5-merous. Hypanthium subglobose, 1.7 mm. long, sparsely short-strigose. Calyx-tube scarcely developed; sepals membranous, broadly triangular with concave margins, 0.5 mm. long from the torus; exterior teeth stout, erect, subconic, projecting about 0.3 mm. Petals narrowly oblong with inflexed margins and cucullate apex, orange, 1.3 mm. long. Stamens isomorphic; filaments stout, 1–2 mm. long; anthers straight, 1.8 mm. long; connective elevated at its base into a conspicuous dorsal protuberance. Ovary two-thirds inferior, 3-celled, glabrous; style 4 mm. long; stigma capitellate.

TYPE: *Klug 1936*, from forest at Umbria, Comisaria del Putomayo, Colombia, alt. 325 m.

Krukoff 10856, from the vicinity of Mapiri, Bolivia, is identical. Since the genus Leandra has received no careful study and its species are not arranged in logical order, it is impossible to discuss the possible relationship of the new species.

Miconia stellulata Gleason, sp. nov. Sect. *Jucunda*. A *Miconia pubicalyci* differt pubescentia ubique multo tenuiore, foliis 5-pli-nerviis, sepalis fere erectis, petalis calyci styloque glabris, dentibus exterioribus crassis triangularibus.

Tree 8 m. high, the branches terete and glabrous, the youngest twigs, petioles, and inflorescence closely and minutely brown-stellate-tomentose. Petioles slender, 10–15 mm. long, deeply and narrowly channeled above. Blades firm, ovate-lanceolate, up to 14 cm. long and 5.5 cm. wide, long-acuminate, entire, rounded at the base, 5-pli-nerved, the principal laterals arising 5–8 mm. from the base and outwardly curved, lightly impressed above, the straight secondaries 3–5 mm. apart, ascending at an angle of about 70°, obscure above; young leaves brown-stellate-tomentose beneath, sparsely stellate above, soon glabrate on both sides. Panicle small, the 5-merous flowers sessile in small glomerules. Hypanthium obconic, 3.7 mm. long to the torus, very thinly and minutely stellate-pubescent. Calyx soon deciduous, scarcely spreading; calyx-tube prolonged 0.7 mm. to acute sinuses, glabrous; sepals broadly depressed-semicircular, 1 mm. long from the torus, with no free margin; exterior teeth triangular, acute, carinate on the inner side, adnate to the sepal and extending 0.9 mm. beyond it. Petals obovate-oblong, 4.2 mm. long, 2 mm. wide, obliquely retuse, glabrous. Stamens isomorphic but differing slightly in size; filaments slender, glabrous, 4 or 4.5 mm. long; anthers subulate, slightly arcuate, 2-celled, opening by a small terminal pore, 3.4 or 3.9 mm. long, the thecae prolonged briefly below the filament; connective simple. Ovary half inferior, 3-celled, the rounded summit glabrous; style slender, glabrous, 10.3 mm. long; stigma truncate.

TYPE: *Krukoff 11376*, from Copacabana, Dept. La Paz, Bolivia, alt. 850–950 m.

It is a member of the species-group within Sect. *Jucunda* characterized by the extraordinary development of the exterior teeth, discussed by me in 1932.[1] To the eight species then known two have since been added. One of these is obviously similar to *M. stellulata* but differs in the characters stated in the diagnosis.

Miconia rosea Gleason, sp. nov. Sect. *Adenodesma*. Rami juniores, petioli, venae mediae, inflorescentia et hypanthia densissime tomentosi; laminae membranaceae ellipticae petiolatae 5-pli-nerviae supra glabrae subtus ad venas sparse stellatae; sepala bene evoluta; stamina dimorpha; antherae subulatae; connectiva basi dilatata secus margines glandulis ornata.

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[1] Bull. Torrey Club **59**: 360–363.

Tree 6–8 m. high, the younger branches densely tomentose with stout conic hairs about 1 mm. long. Petioles stout, 2–5 cm. long, tomentose like the stem. Blades thin, green on both sides, elliptic, 16–26 cm. long, 8–14 cm. wide, abruptly acuminate, repand-denticulate, cordulate at the rounded base, 5-plinerved, glabrous above with obscure plane veins spreading at nearly right angles, very sparsely stellate on the veins beneath. Panicle few-flowered, sparsely branched, 13 cm. long. Flowers 5-merous, sessile but apparently on pedicels 5–8 mm. long. Hypanthium hemispheric, 4.2 mm. long to the torus, very thick-walled, densely tomentose. Calyx-tube flaring, 2.3 mm. long, sparsely sericeous within; sepals broadly triangular from acute sinuses, 3.1 mm. long from the sinus, sericeous within, pubescent outside like the hypanthium; exterior teeth minute inconspicuous thickenings. Petals coriaceous or fleshy, elliptic-oblong, 16 mm. long, 8.5 mm. wide, slightly inequilateral. Small stamens: filaments stout, 7.5 mm. long, finely pubescent; anthers slightly arcuate, subulate, 6.6 mm. long, with convolute thecae; connective widened below and extending over half the sides of the thecae, bearing near its margin 6–10 short-stipitate glands. Large stamens: filaments 9 mm. long, pubescent as before; anthers slightly sigmoid, subulate, 7.5 mm. long, the thecae slightly convolute; connective expanded at base over the whole sides of the thecae and bearing around its margin 12–20 nearly sessile glands. Ovary mostly inferior, 5-celled, with a terminal erect glabrous collar 1 mm. high; style straight, 16 mm. long, finely pubescent; stigma truncate.

TYPE: *Cárdenas 762,* from Chimore, Río San Rafael, Cochabamba, Bolivia, in damp forest, alt. 800 m.

The structure of the anther places the species at once in the section *Adenodesma* and adjacent to *M. axinaeoides* Gl., also from Bolivia. It resembles this species in general habit, except its long petioles, but differs from it in its pubescence, its well-developed sepals, and the shape of the connective. A better knowledge of *M. Urbaniana* Cogn., of southern Peru, may eventually show that it is also related here, although assigned by its author to Sect. *Eumiconia.*

Miconia barbicaulis Gleason, sp. nov. Sect. *Amblyarrhena.* Rami stellato-puberuli et longissime purpureo-setosi; folia longe petiolata subtus purpurea late ovata, breviter acuminata, basi subcordata, 7-nervia, supra hirsutula subtus mox glabra; panicula laxa pauciflora, nodis setosis; flores 5-meri; calyx calyptratus demum in lobos irregulariter ruptus; stamina isomorpha leviter connata; antherae 4-loculares, connectivo basi in lobum dorsalem producto.

Shrub 12 dm. high, the younger stems 4-sulcate, sparsely setose with spreading or deflexed blue hairs up to 12 mm. long. Petioles 5–7 cm. long, pubescent like the branches. Blades thin, broadly ovate, 20–25 cm. long, 15–17 cm. wide, short-acuminate, toothed and ciliate, subcordate, 7-nerved, hirsutulous above, hirsute beneath when young, soon glabrescent. Panicle 12 cm. long, loose, few-flowered, long-setose at the nodes. Flowers 5-merous. Hypanthium subglobose, 2.2 mm. long to the torus, sparsely long-setose. Calyx calyptrate, membranous, 2.6 mm. long, at maturity divided into irregular lobes, sparsely setose; exterior teeth spreading from the middle of the lobes, subterete, 1 mm. long. Petals pale rose, ovate-oblong, 3 mm.

long, 2 mm. wide, obtuse, entire, scarcely inequilateral. Stamens isomorphic, coherent in a ring; filaments broad and flat, 1.4 mm. long; anthers stout, radially flattened, blunt, 1.4 mm. long, 4-celled, opening by a minute terminal pore; connective elevated into a ridge over the thecae and prolonged at base into a flat rhombic dorsal appendage 0.6 mm. long. Ovary wholly inferior, 3-celled; style 3 mm. long; stigma capitellate.

TYPE: *Skutch 4420,* from vicinity of Puyo, Napo-Pastaza, Ecuador, alt. 750–1000 m.

The anthers are distinctly those of the section *Amblyarrhena,* and the same kind of connective occurs in *M. acalephoides* Naud. The only species of the section which it resembles in general appearance are *M. cardiophylla* Cogn., *M. Lechleri* Triana and *M. plumifera* Triana, which have glomerate flowers, unappendaged anthers, and normal calyx. The calyptrate calyx suggests the section *Laceraria,* in which *M. Wagneri* Macbride has a similarly prolonged connective but differs in its anthers, exterior teeth and foliage.

Miconia mapirensis Gleason, sp. nov. Sect. *Amblyarrhena.* Rami dense substrigosi pilis inflexis; folia breviter petiolata elliptica breviter acuminata basi rotundata sub-5-pli-nervia, utrinque brevissime setulosa; inflorescentia paniculata ramosa; floribus 5-meris in glomerulos dense aggregatis; hypanthium hirsutum; sepala rotundata, dentibus exterioribus triangularibus adpressis; filamenta dense glandulosa; antherae 4-loculares incurvae, connectivo simplici; ovarium 4-loculare; stigma late capitatum.

Small tree, 8 m. high. Younger branches terete, densely substrigose with incurved stiff hairs. Petioles 10–15 mm. long, pubescent like the stem. Blades firm, elliptic, 12–16 cm. long, 4.5–6 cm. wide, short-acuminate, entire, rounded at base, sub-5-pli-nerved, setose on both sides, more densely beneath, with hairs like those of the stem; secondary veins about 5 mm. apart, ascending at an angle of about 75°. Panicle short-peduncled, 10–12 cm. long, freely branched, the axis and spreading branches densely substrigose. Flowers 5-merous, densely aggregated into terminal glomerules, on pedicels 1–1.5 mm. long, subtended by linear orange-red bracts 2 mm. long. Hypanthium short-cylindric, 2.8 mm. long to the torus, densely hirsute. Sepals broadly rounded, 1.5 mm. long from the torus; exterior teeth triangular, appressed, rather fleshy, half as long as the sepals, mostly adnate. Petals broadly elliptic, 2.8 mm. long, broadly retuse. Stamens isomorphic; filaments stout, flattened, 2.6 mm. long, densely stipitate-glandular; anthers stout, incurved, 2.6 mm. long, 4-celled; connective simple. Ovary two-fifths inferior, 3-celled, the free summit conic, sharply 10-ribbed, extended as 10 connate lobes surrounding the style; style stout, villosulous, 6.5 mm. long; stigma depressed-capitate, 1.7 mm. wide.

TYPE: *Krukoff 11215,* from Copacabana, Dept. La Paz, Bolivia, alt. 850–950 m. Another sheet from the same locality is *Krukoff 11188.*

Miconia mapirensis is a member of a small group of Andean species characterized by glandular filaments, incurved anthers, broad stigmas, and glomerate flowers and including *M. modica* Gl. and *M. lasiostyla* Gl. with stellate pubescence, *M. amabilis* Cogn. with nearly glabrous stem and stellate-

pubescent hypanthium, and *M. Bangii* Cogn., which is nearly or quite glabrous throughout. In all of these the inner pair of veins leave the midvein at an acute angle, while the outer pair are curved into the perimeter of an ellipse. *M. sanguinea* Triana also shares these characters except as to inflorescence; its flowers are long-pedicelled.

Miconia megastigma Gleason, sp. nov. Sect. *Amblyarrhena.* Rami hirsuti et stellati; folia breviter petiolata, ovato-oblonga, breviter acuminata, basi rotundata vel subcordata, 5-pli-nervia, primo utrinque pubescentia mox glabra; panicula pauciramosa; flores 5-meri; hypanthium stellatum et setosum; sepala late triangularia; petala late ovata; stamina paulo dimorpha; filamenta lata glandulosa; antherae obovoideae, connectivo ser. ext. in appendicem dorsalem producto; stylus glandulosus; stigma latum peltatum.

Slender vine climbing by roots, the younger stems terete, hirsute (hairs 1.5–2 mm. long) and minutely stellate. Petioles about 1 cm. long, pubescent like the stem but more densely. Blades oblong, up to 10 cm. long by 6 cm. wide, short-acuminate, entire or nearly so, ciliate at least when young, rounded or subcordate at base, 5-pli-nerved, minutely stellate above when young, soon glabrous, paler and glabrous beneath. Panicle about 1 dm. long, pubescent like the stem, its few branches spreading at right angles. Flowers 5-merous. Hypanthium hemispheric, 2 mm. long, nearly 4 mm. wide, minutely stellate and sparsely long-setose. Calyx-tube not prolonged; sepals horizontally spreading, broadly triangular, nearly 1 mm. long, more than 2 mm. wide; exterior teeth stoutly subulate, appressed, exceeding the sepals. Petals white, thick and fleshy, broadly ovate, 4 mm. long, essentially symmetrical. Episepalous stamens: filaments 1.8 mm. long, 1.3 mm. wide, sparsely glandular on the margin; anthers obovoid, 2.1 mm. long, 4-celled; connective expanded at base into a transversely elliptic fleshy dorsal lobe 0.6 mm. long, 1.3 mm. wide. Epipetalous stamens: filaments as before, but slightly narrower, densely glandular on the back only; anthers as before; connective scarcely prolonged, truncate. Ovary nearly inferior, 5-celled; style 4 mm. long, densely glandular; stigma peltate, 5-lobed, 2.4 mm. wide.

TYPE: *Skutch 4558*, from vicinity of Puyo, prov. Napo-Pastazo, Ecuador, alt. 750–1000 m.

The species is undoubtedly related to *M. Killipii* Gl., to which it bears a strong superficial resemblance. The latter is a tall shrub with circular stigma and unappendaged isomorphic anthers.

Miconia Skutchii Gleason, sp. nov. Sect. *Amblyarrhena.* Rami dense tomentosi sub setis aureis longis; folia longe petiolata cordato-ovata, usque 22 cm. longa 16 cm. lata, acuminata, dentata, 9-nervia, supra setosa subtus molliter pubescentia. Panicula gracilis; flores 5-meri; hypanthium dense villosum; sepala semicircularia hyalina; stamina isomorpha, connectivo infra thecas breviter producto late dilatato.

Shrub 7 dm. high, the younger branches deeply 4-sulcate, densely tomentose with minute pale hairs, densely hirsute with golden bristles to 2 mm. long. Petioles stout, pubescent like the stem, nearly half as long as the blades. Leaf-blades minutely puberulent above and setose with golden hairs to 2 mm.

long, beneath softly pubescent with very slender hairs 0.3 mm. long. Panicle slender, 15 cm. long, the lower branches 2 cm. long. Flowers nearly sessile, glomerate, 5-merous. Hypanthium 3.7 mm. long to the torus, very densely lanate with spreading hairs to 1.5 mm. long. Calyx erect, the tube prolonged 0.7 mm., pubescent like the hypanthium; sepals semicircular, hyaline, 1.4 mm. long from the torus, minutely erose-ciliate; exterior teeth wholly adnate, projecting 0.6 mm. Petals oblong, 5.5 by 2.8 mm., white, essentially symmetrical. Stamens isomorphic; filaments slender, 2.5 mm. long, obscurely geniculate near the summit; anthers oblong, 2.1 mm. long, 4-celled; connective thickened and widened toward the base, prolonged 0.6 mm. below the thecae into a thick, obscurely 3-lobed appendage. Ovary nearly inferior, 5-celled, glabrous; style straight, 6 mm. long; stigma punctiform.

TYPE: *Skutch 4519,* from vicinity of Puyo, prov. Napo-Pastaza, Ecuador, alt. 750–1000 m.

Comparatively few other species of this section of *Miconia* have cordate leaves, and in none of them is the pubescence so dense. It varies in our plant from extremely delicate hairs only 0.2 mm. long through all intermediate stages to fairly stiff bristles 2 mm. long, producing a golden indument over the stem, petioles, panicle and hypanthium.

Miconia chrysocoma Gleason, sp. nov. Sect. *Cremanium.* Frutex, ramis hirsutis; folia inter minores, flavo-viridia, oblonga vel oblongo-lanceolata, argute denticulata, saepe ciliata, 5-pli-nervia, subtus ad venas villosa; panicula aureo-hirsuta; flores breviter pedicellati glomerati; hypanthium aureo-villosum; stamina isomorpha, connectivo basi breviter 3-lobo; stigma obconicum.

About a meter high; upper branches densely brown-hirsute with stoutish, rather flexuous, spreading hairs 1–2.5 mm. long, beneath the hairs somewhat pulverulent. Petioles stout, hirsute like the stem, 10–15 mm. long. Blades firm, yellow-green, oblong-lanceolate or oblong, up to 9 by 3 cm., subacuminate, sharply denticulate with shallow upcurved teeth alternating with single cilia, rounded at the base, 5-pli-nerved, the outer pair submarginal, glabrous above, villous beneath on the primaries, less so on the secondaries and nearly glabrous on the surface. Panicle nearly sessile, about 10 cm. long, hirsute with yellow hairs; pedicels 1 mm. long. Flowers glomerate, 5-merous. Hypanthium subglobose, 2 mm. long to the sinus, loosely villous. Calyx-lobes nearly semicircular from acute sinuses, 0.4–0.5 mm. long, very thin; exterior teeth equal in width but half as long, slightly spreading. Petals broadly elliptic, retuse, white, 1.8 mm. long. Stamens isomorphic; filaments 2.2 mm. long; anthers 1.2 mm. long, opening by two wide terminal pores, the connective prolonged below into a dorsal and two ventral lobes 0.2–0.3 mm. long.

TYPE: *Killip & Smith 18035,* from La Baja, Dept. Santander, Colombia, alt. 2700–3500 m.; *Cuatrecasas 1149* and *1742,* from Boyaca, are the same.

Through the artificial key in Cogniaux' monograph, our species appears to be related to *Miconia divergens* Triana, a larger plant with much larger entire leaves and capitate stigma.

Clidemia Killipii Gleason, sp. nov. Sect. *Calophysa.* Rami glanduloso-hirsuti; petioli formicario hirsuto tecti; laminae magnae falcatae breviter acuminatae, basi oblique cordulatae; flores 5-meri; hypanthium glandulosum; sepala rotundato-triangularia, dentibus exterioribus toto adnatis subulatis, sepala breviter excedentibus; antherae anguste subulatae inappendiculatae; ovarium corona ornatum.

Shrub about a meter high, the upper branches densely glandular, the hairs to 2.5 mm. long, flattened at the base. Petioles 1 cm. long or less, the lower side completely covered by a sparsely hirsute convolute formicarium. Blades oblong-elliptic or oblong-obovate, essentially isomorphic, to 23 cm. long by 12 cm. wide, abruptly short-acuminate, irregularly denticulate, obliquely cordulate at base, 3-pli-nerved with an additional marginal pair, hirsute above, hirsute on the veins beneath, the hairs partly glandular. Panicles axillary, slender, glandular-hirsute, 14–18 cm. long, the lateral branches 1–2 cm. long. Flowers 5-merous, short-pedicelled. Hypanthium tubular-urceolate, dilated at the base, 3.8 mm. long to the torus, glandular-hirsute, the hairs to 1.7 mm. long. Calyx-tube nearly erect, 0.7 mm. long. Sepals rounded-triangular, 1–1.1 mm. long from the torus, obtuse; exterior teeth glandular like the hypanthium, stoutly subulate, adnate to the end of the sepal, projecting about 0.6 mm. Petals light green, oblong-elliptic, 5.2 mm. long, retuse, slightly inequilateral. Stamens essentially isomorphic; filaments slender, 5.2 mm. long; anthers subulate, 5.3 mm. long, opening by a ventro-terminal (outer series) or dorso-terminal (inner series) pore. Ovary 5-celled, half-inferior, the rounded glabrous summit prolonged into a terete crown 0.4 mm. high; style nearly straight, 4.3 mm. long; stigma punctiform.

TYPE: *Killip 35249,* from dense forest on a ridge along the Yeracüí Valley, Corcovada Region, Intendencia El Chocó, Colombia, alt. 200–275 m.

While definitely related to *C. juruensis* (Pilger) Gl., *C. foliosa* Gl. and *C. heterophylla* (Desr.) Gl. (cf. Bull. Torrey Club **58**: 79–85. 1931), our species is distinguished from each of them by exceptionally strong characters. All three have sessile or very short flower-clusters; in the second and third the leaves are dimorphic; in the first the ovary is setose, and several other less conspicuous but equally important characters distinguish them from *C. Killipii.*

Clidemia Pittieri Gleason, sp. nov. Sect. *Calophysoides.* Habitu *Clidemiae gracilis* Pitt. similis et illa forsan affinis, differt caulibus teretibus, foliis amplexicaulibus, antheris late dolabriformibus 4-locularibus.

Small tree to 8 m. tall (according to Woodson), with terete twigs, glabrous throughout. Leaves sessile, cordate-clasping, abruptly acuminate, otherwise strongly dimorphic, the larger ovate-lanceolate, 8–15 cm. long, 3–7 cm. wide, 5-nerved with an additional weak marginal pair, the smaller broadly ovate to rotund, 2–3 cm. long and nearly or quite as wide. Cymes from the axils of the upper large leaves, few-flowered, 3–6 cm. long, pedunculate, trichotomous, the very slender branches subtended by linear bracts 6–2 mm. long. Flowers 5-merous, Hypanthium subglobose, fleshy, reddish, 3.3 mm. long to the torus. Calyx-tube fleshy, somewhat flaring, prolonged about 0.4 mm. to very broad sinuses; sepals broadly depressed-triangular, about 0.6 mm. long; exterior teeth adnate for about half their length, resembling the sepals in shape but smaller. Petals red, subrotund, 4 mm. long and wide, inequilateral, shallowly retuse, 9-nerved. Stamens isomorphic; filaments stout, nearly 2 mm. long; anthers stout, 1.3 mm. long and nearly as wide, 4-celled; connective elevated in the lower half into a prominent dorsal ridge, unappendaged. Ovary three-fourths inferior, 5-celled, its summit truncate-conic; style stout, 4.5–5 mm. long; stigma truncate.

TYPE: *Pittier 3177*, from Prov. Chiriqui, Panama, alt. about 1700 m.; also collected more recently in the same province by *Woodson & Schery, 289* and *562*.

This remarkable plant has been known to me for several years and has been left undescribed because its anthers are so unlike those of the other species of *Clidemia*. In all other features it agrees with that genus. It is distinguished from *C. gracilis* Pitt. at a glance by its cordate-clasping leaves.

Ossaea spicata Gleason, sp. nov. Sect. *Bractearia*. Frutex ramis tomentosulis; laminae breviter petiolatae oblanceolatae caudato-acuminatae 3-nerviae, supra glabrae subtus ad venas subtomentosae; flores sessiles in glomerulis spicatis, bracteati; hypanthium subtomentosum; sepala scariosa dentibus exterioribus vix evolutis; petala dorso lepidoto-stellata; antherae basi in calcar breve productae.

Shrub 3–4 m. high, the younger branches slender, thinly tomentose. Petioles 5–10 mm. long, pubescent like the stem and setose toward the base on the upper side. Blades thin, oblanceolate, paler beneath, 12–18 cm. long, 4–6 cm. wide, caudate-acuminate (acumen linear, obtuse, 10–15 mm. long), repand-denticulate, narrowed from above the middle to an acute base, 3-nerved, with an additional pair of submarginal veins, glabrous above, thinly subtomentose beneath on the primary veins only. Flowers 5-merous, sessile in small glomerules subtended by oblong to ovate bracts 1–1.5 mm. long, separated by internodes 10–15 mm. long, forming a straight, axillary or terminal, interrupted spike. Hypanthium cup-shape, 1.6 mm. long to the torus, thick-walled, subtomentose. Calyx-tube nearly erect, 0.5 mm. long; sepals very thin, broadly ovate to triangular, 1.2 mm. long from the torus; exterior teeth minute thickened triangles. Petals erect, lanceolate, 4.4 mm. long, lepidote-stellate on the back, the minute subulate exterior teeth erect, the actual apex cucullate and minutely inflexed. Anthers linear, 1.4 mm. long; connective prolonged at base into a lanceolate, erose, dorsal lobe about 0.4 mm. long. Ovary 3-celled, glabrous; style straight, glabrous; stigma apparently punctiform.

TYPE: *Killip 35166*, collected in dense forest between Quebrada Guarapo and Mandinga, Intendencia El Chocó, Colombia, alt. 120–180 m.

In its spicate bracted inflorescence *O. spicata* is clearly related to *O. rufibarbis* Triana, which is a much more robust plant, with pli-nerved leaves, long-hirsute inflorescence, and much larger bracts.

THE NEW YORK BOTANICAL GARDEN,
NEW YORK, NEW YORK

THREE NEW SPECIES OF MEXICAN UMBELLIFERAE

MILDRED E. MATHIAS AND LINCOLN CONSTANCE

Arracacia ternata Mathias & Constance, sp. nov. Herba gracilis caulescens e radice horizontali crassa ramosa, 6–10 dm. alta, omnino glabra vel minute scaberula; folia in ambitu deltoidea, 1.5–3 dm. longa, 3–4-ternata, foliolis ovato-lanceolatis apice acutis, basi cuneatis, terminalibus exceptis distinctis petiolulatis sessilibusve, 2–5 cm. longis, 1–2 cm. latis, crasse dentatis lobatisque, dentibus triangularibus mucronatis; petioli gracillimi, 5–15 cm. longi, basi vaginantes; folia caulina pauca foliis basilaribus similia, insuper demum multo reductis uni- vel plurilobatis, lobis elongatis filiformibus, 1–2 cm. longis, vaginis obsoletis; inflorescentia ramosa pedunculis infimis alternis, superioribus verticellatis gracilibus patenti-adscendentibus subaequalibus, 2–3.5 cm. longis; radii fertiles 5–6 graciles patenti-adscendentes subaequales, 2–3.5 cm. longi; pedicelli fertiles 1–5, graciles patenti-adscendentes, 3–6 mm. longi; flores purpurei, petalis ovalibus; stylopodium breviconicum, disco conspicuo crenulato, stylis brevibus divergentibus recurvatisve; carpophorum usque ad basim bifidum; fructus oblongus, 7–12 mm. longus, 2–3 mm. latus, glaber, apice basique attenuatus, apice emarginatus, costis filiformibus; vittae parvae in intervallis 1–2, in commissuris 4; seminis facies profunde sulcata.

Slender caulescent, branching perennial from a stout, horizontal woody root, 6–10 dm. high, glabrous throughout or the foliage minutely scaberulous; leaves deltoid in general outline, excluding the petioles 1.5–3 dm. long, 3–4-ternate, the leaflets ovate-lanceolate, 2–5 cm. long, 1–2 cm. broad, acute at apex, cuneate at base, all but the terminal distinct, coarsely toothed and lobed with triangular-mucronate teeth, petiolulate or sessile; petioles very slender, 5–15 cm. long, sheathing at base; cauline leaves few, like the basal, the uppermost greatly reduced and consisting of 1–several elongate, filiform lobes 1–2 cm. long, the sheaths obsolete; inflorescence freely branched, the lower peduncles alternate, the upper verticillate, slender, 3–6 cm. long, often with a small sterile lateral umbel; involucre wanting, or of a solitary foliaceous linear bract; involucel of 1–several linear bractlets, 3–5 mm. long, exceeding the flowers; fertile rays 5–6, slender, spreading-ascending, subequal, 2–3.5 cm. long; fertile pedicels 1–5, slender, spreading-ascending, 3–6 mm. long; flowers purple, the petals oval; stylopodium low-conical, with a conspicuous crenulated disk, the styles short, divergent or recurved; carpophore 2-cleft to the base; fruit oblong, 7–12 mm. long, 2–3 mm. broad, glabrous, tapering at each end, and with a V-shaped notch at the apex, the ribs filiform; oil tubes small, 1–2 in the intervals, 4 on the commissure; seed face deeply sulcate.

Type specimen: Bartlett 10294, Cerro Parrena, vicinity of San José, Sierra de San Carlos, Tamaulipas, Mexico, alt. 3100 ft., July 13, 1930 (MBG[1] TYPE, US).

This species is known only from the type collection. It is most closely related to *Arracacia fruticosa* and *A. Pringlei*. *Arracacia fruticosa* is a woody species and *A. Pringlei* is characterized by mostly alternate peduncles, longer involucel bracts, more numerous rays, shorter pedicels and white or cream-colored flowers.

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[1] The institutions in which these specimens are deposited are designated as follows: Royal Botanic Gardens, Kew, K; Missouri Botanical Garden, MBG; New York Botanical Garden, NY; United States National Herbarium, US.

Donnellsmithia Hintonii Mathias & Constance, sp. nov. Herba annua vel biennis, 6–12 dm. alta, e radice simplice gracile, foliis nodisque paullo scaberulis; folia in ambitu deltoidea, 6–12 cm. longa, ternato-pinnate dissecta, segmentis terminalibus plerumque distinctis, foliolis lanceolatis ovatisve, 10–30 mm. longis, 5–15 mm. latis, basi cuneatis, pinnatifidis dentatisque lobulis (dentibus) integris, apiculatis glabratis venis rachibusque minute scaberulis; petioli 5–15 cm. longi; folia caulina summa alterna decussatave; umbellae crebro sessiles vel plerumque pedunculatae, pedunculis alternis, 0.5–3 cm. longis; involucrum nullum vel unibracteatum; involucellum nullum; radii 3–6, subaequales, 0.6–1.2 cm. longi; pedicelli fertiles 1–4, 2–6 mm. longi, sterilibus longiores; flores flavi; stylopodium manifestum breve; fructus orbicularis obcordatusve, 1.5 mm. longus, 1.5–2 mm. latus; basi cordatus ad apicem versus attenuatus glaber, apice rotundo, costis filiformibus indistinctis; vittae commissurarum ut eae in intervallis 2–4; seminis facies vadose sulcata.

Annual or biennial from a slender taproot, 6–12 dm. high, the foliage and nodes slightly scaberulous; leaves deltoid in general outline, excluding the petioles 6–12 cm. long, ternate-pinnately dissected, the leaflets lanceolate to ovate, 10–30 mm. long, 5–15 mm. broad, mostly distinct, attenuate at apex, cuneate at base, pinnatifid and toothed with entire, apiculate lobes or teeth, minutely scaberulous on the veins and the rachis or glabrate; petioles 5–15 cm. long; uppermost cauline leaves alternate or opposite; peduncles alternate, 0.5–3 cm. long, or some umbels frequently sessile; involucre wanting, or of a single bract; involucel wanting; rays 3–6, subequal, 0.6–1.2 cm. long; fertile pedicels 1–4, 2–6 mm. long, longer than the sterile pedicels; flowers yellow; stylopodium low but evident; fruit orbicular to obcordate, 1.5 mm. long, 1.5–2 mm. broad, cordate at base, rounded but tapering toward apex, glabrous, the ribs filiform, indistinct; oil tubes 2–4 in the intervals and on the commissure; seed face shallowly sulcate.

Type specimen: Hinton 8463, oak woods, Salitre, District of Temascaltepec, State of Mexico, September 19, 1935. (NY TYPE, K).

Specimens examined: MEXICO: llano, Tenayac, 1650 m., *Hinton 4851* (K, NY); barranca, Tenayac, *Hinton 8367* (K, NY); hill, Mina de Agua, 1990 m., *Hinton 2329* (K, NY); Puerto Salitre, 1300 m., *Hinton 1795* (K).

This species is separated from *Donnellsmithia mexicana* by its shallowly sulcate seed face, the fertile pedicels much longer than the sterile, and the pinnatifid and toothed leaflets. Both *D. Hintonii* and *D. mexicana* are readily separable from *D. biennis* by the evident stylopodium, oil tubes several in the intervals, fruit tapering at the apex, and the indistinct ribs.

Prionosciadium simplex Mathias & Constance, sp. nov. Herba perennis caulescens erecta, 8 dm. alta, usque ad inflorescentiam scaberulam omnino glauca glabraque, folia basilaria in ambitu deltoidea, 8–15 cm. longa, biternata, foliolis glabris distinctis petiolulatis subtus glaucis, 1.5–2.5 cm. longis, 0.8–1.5 cm. latis, oblongis ovato-lanceolatisve serrulatis, obtusis vel apice

abrupte acutis, basi truncatis lobis duobus lateralibus instructis; petioli graciles, 3–5 cm. longi, vaginis elongatis oblongis marginibus scariosis; folia caulina foliis basilaribus similia alterna sursum reducta, vaginis conspicuis oblongis; inflorescentiae umbella unica terminalis, interdum ramis lateralibus instructis; pedunculus gracilis, 10–12 cm. longus; involucrum nullum; involucelli bracteolae plures lanceolatae ovato-lanceolataeve acuminatae purpurascentes scaberulae, 3–6 mm. longae; petala purpurea obovata, circa 2 mm. longa; stylopodium depressum, stylis longiusculis; fructus immaturus oblongus basi rotundus, apice truncatus, 6–8 mm. longus, 3–3.5 mm. latus, glaber, dorsaliter valide compressus, costis dorsalibus filiformibus, lateralibus tenui-alatis, alis corpore angustioribus.

Rather slender, caulescent, erect perennial, 8 dm. high, glaucous and glabrous throughout except for the scaberulous inflorescence; basal leaves deltoid in general outline, excluding the petiole 8–15 cm. long, biternate, the leaflets oblong to ovate-lanceolate, distinct, 1.5–2.5 cm. long, 0.8–1.5 cm. broad, obtuse or abruptly acute at apex, truncate at base, finely serrate and often with two lateral lobes at base, glaucous beneath, petiolulate; petioles slender, 3–5 cm. long, the sheaths elongate, oblong with a scarious margin; cauline leaves like the basal, alternate, reduced upwards with a conspicuous oblong sheath; inflorescence of a single terminal umbel or with some lateral branches below; peduncle slender, 10–12 cm. long; involucre wanting; involucel of several lanceolate or ovate-lanceolate, acuminate, purplish bractlets, 3–6 mm. long, shorter than the fruit; fertile rays about 10, spreading-ascending, unequal, 1.5–4.5 cm. long; fertile pedicels 2–6, spreading-ascending, 2–4 mm. long; calyx teeth obsolete; petals purple, obovate, with an inflexed tip, about 2 mm. long; stylopodium depressed, the styles rather long; ovaries glabrous; immature fruit oblong, 6–8 mm. long, 3–3.5 mm. broad, rounded at base, truncate at apex, glabrous, strongly flattened dorsally, the dorsal ribs filiform, wingless, the laterals thin-winged, the wings (in young fruit) narrower than the body.

Type specimen: Nelson 4478, on mountains near Miquihuana, Tamaulipas, Mexico, alt. 7000–9000 ft., June 10, 1898 (US 332,526 TYPE).

Prionosciadium simplex is most nearly allied to *P. humile*, which is itself anomalous in the genus. Both species are characterized by their low slender stature and comparatively simple inflorescence. *Prionosciadium simplex* may be separated from *P. humile* by the finely serrate, oblong to ovate-lanceolate leaflets, 1.5–2.5 cm. long, 0.8–1.5 cm. broad, and the purple flowers.

UNIVERSITY OF CALIFORNIA
BERKELEY, CALIFORNIA

INDEX TO AMERICAN BOTANICAL LITERATURE

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

Papers that relate exclusively to bacteriology, forestry, agriculture, horticulture, manufactured products of vegetable origin, or laboratory methods are not included. If users of the Index will call the attention of the editor to errors or omissions, their kindness will be appreciated.

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BULLETIN
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STUDIES IN THE GENUS PHYSALACRIA[1]

GLADYS E. BAKER

(WITH ONE HUNDRED AND FIVE FIGURES[2])

The genus *Physalacria* is generally regarded as a member of the family *Clavariaceae* (Killerman in Engler and Prantl 1928; Coker 1923; Clements and Shear 1931), although more recently the suggestion that it be transferred to a place amongst the *Thelephoraceae* has been advanced (McGuire 1939). This proposal is based upon the assertion that the hymenium occupies a unilateral and inferior positon instead of being amphigenous, which is the usual hymenial characterization for the *Clavariaceae.* McGuire has convincingly demonstrated the fallacy of the amphigenous distribution in *Physalacria* and has pointed out also the erroneous conclusions of previous investigators who followed this assumption. Up to now very little attention has been devoted to detailed studies of any of the *Clavariaceae*. Wakyama (1932) mentions the basidia of *Clavaria* briefly, but only as a prelude to studies never completed. A comprehensive treatment of *Typhula* has just appeared (Remsberg 1940), but without the inclusion of cytological data. Apparently *Physalacria* has not been investigated cytologically. In order to ascertain with any certainty the approximate positon of this genus and its relationships, a complete study of the basidiocarp development and differentiation seems necessary.

Despite the fact that this genus has been defined clearly enough for recognition for over fifty years (Peck 1882), collections of this attractive little genus are still infrequent. A number of collections have been made in the intervening years, chiefly in the eastern part of the United States and Canada. The material serving as a basis for this study was collected July 25 and July 27, 1935, from basidiocarps growing on a decaying stump in Door County, Wisconsin. At that time the fructifications were prolific but in subsequent seasons they failed to appear although the stump was carefully watched during the summers of 1936 and 1938. The summer of 1936 was an

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exceptionally dry one but even after the beginning of the rainy season the fungus did not reappear.

The material was fixed and preserved in formol-acetic-alcohol. Later characteristic stages of development were selected for sketching, and, in turn, sectioning. All material was dehydrated in a butyl-alcohol series previous to imbedding, and serial sections 3, 5, 8, and 10 μ thick were cut. Slides were stained with Heidenhain's iron-alum-haematoxylin and counter-stained with phloxine. Temporary mounts were examined in a lacto-phenol preparation with a combination of cotton-blue and acid fuchsin as stains.

The youngest stage sectioned revealed a scarcely differentiated ball of tissues partially imbedded in the wood cells of the substratum (fig. 1). Hyphal filaments with no special orientation abundantly pack the lumens of the wood cells at this and later stages (fig. 2). The hyphae appear to be binucleate. Basally the filaments are compactly arranged, forming a zone of thin-walled pseudo-parenchyma (fig. 3). Inside the hyphal cells the cytoplasm forms a scant lining, and the nuclei, when apparent, are in close association or are scattered. Above the basal tissue the hyphae often appear as longer cells although their pseudo-parenchymatous nature is not lost completely (fig. 4). A short distance below the surface of the basidiocarp the cell arrangement becomes briefly reticulated before passing into the long loose hyphae which radiate freely over the surface. The hyphal tips are completely undifferentiated (fig. 5).

When the distinction between stalk and head of the fructification is first visble, the tissues are fundamentally the same as in the button stage although they are now present in larger amounts (figs. 6, 7). Active cell division in all parts of the developing basidiocarp allows for its growth and subsequent tissue differentiation. The enlarging head is formed of reticulate filaments and free surface hyphae. Already much elongated at this stage, the stalk is composed of cells with nuclei in active divsion as well as in conjugate pairs

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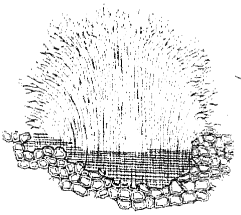
Explanation of figures 1–14

All figures were drawn with the aid of an Abbé camera lucida.

Physalacria inflata. FIG. 1. Section of a young basidiocarp growing on wood. Diagrammatic. ×47. FIG. 2. Detail of wood cells of substratum showing the lumens filled with fungous hyphae. ×550. FIG. 3. Cells from pseudo-parenchymatous zone at base of the basidiocarp illustrated in fig. 1. ×937. FIG. 4. Cells from the interior of the basidiocarp shown in fig. 1. ×937. FIG. 5. Free hyphae from the surface of the same basidiocarp. ×937. FIG. 6. Habit sketch of a young basidiocarp, the head region barely distinguished. ×18. FIG. 7. Section of basidiocarp shown in fig. 7. ×20. FIG. 8. Basal cells of basidiocarp of fig. 7. Note thickening of walls. ×937. FIG. 9. Stalk hyphae from same basidiocarp. ×1550. FIG. 10. Cells from the region of junction between head and stalk. ×937. FIG. 11. Diagrammatic view of a longitudinal section through a developing basidiocarp. ×47. FIG. 12. Reticulate hyphae from the head of the basidiocarp in fig. 11. ×937. FIG. 13. Hyphae from the surface of a young basidiocarp in the future fertile area. ×937. FIG. 14. Hyphae from the surface of a young basidiocarp in the future sterile area. ×937.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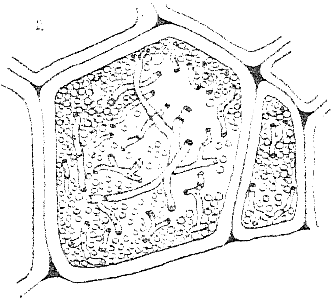
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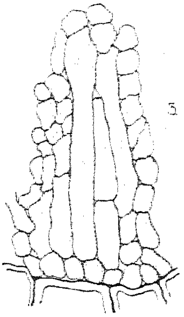
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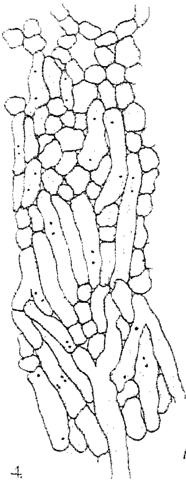
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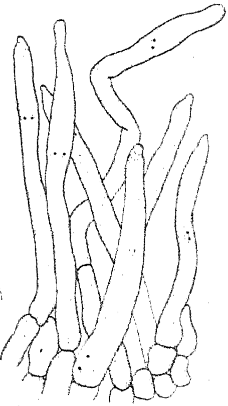
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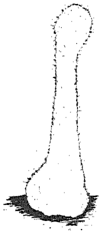
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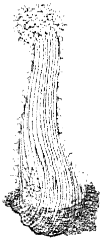
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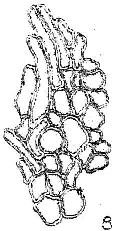
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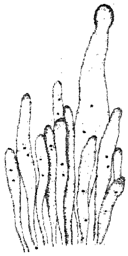
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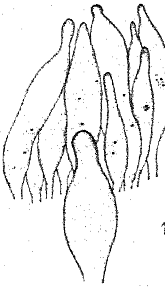
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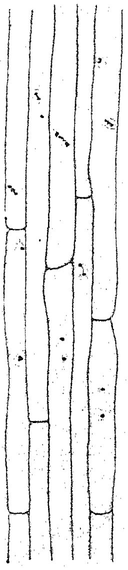
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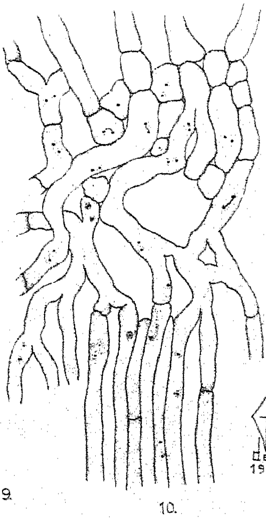
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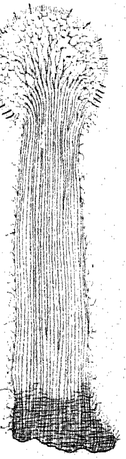
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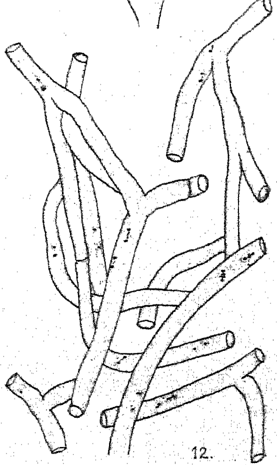
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(fig. 9). The cells are thin-walled, elongated, and mostly are arranged in a compact parallel fashion, although occasionally they are branched. Those toward the outside often are of greater diameter than the internal ones. The walls of the pseudo-parenchymatous cells at the base of the stalk are slightly thickened (fig. 8). In a succeeding stage in the region where the head and stalk tissues adjoin, the reticulate portion becomes much anastomosed and consequently is difficult to trace. Here, too, the nuclei are commonly found to be dividing (fig. 10). The bulk of the head is a loose reticulum of hyphae (fig. 12) which now supports a compact layer of cells on the surface; this results in a smooth head without gyrations (figs. 11, 15). The peripheral hyphae lie parallel to each other in a palisade arrangement. They may be of unequal lengths, but they are usually binucleate and are supported basally by a layer of more closely interwoven cells. In places the hyphal ends are inflated and show a decreasing cytoplasmic content; these are young cells which later will comprise the bulk of the sterile tissues of the head. Cells of the fertile parts are much smaller, filled with dense cytoplasm, and are more or less clavate in shape. Sterile and fertile areas consequently become recognizable long before the basidiocarp is morphologically mature (figs. 13, 14). Occasional cells may have already matured into cystidia, and a few of these may be emergent, but many of them are still disposed well within the tissues. Externally the stalk, from its earliest inception, appears tomentose because of many such inflated cells which terminate free marginal hyphae along its entire length. These hyphae are identical in appearance and nuclear history with the inflated cystidia of the cap (figs. 58, 59). Possibly

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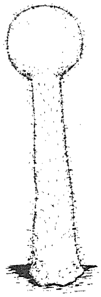
Explanation of figures 15–30

Physalacria inflata. FIG. 15. Young basidiocarp with head and stalk distinct. ×47. FIG. 16. Section of same basidiocarp in diagrammatic longitudinal view, showing the first separation of reticulate tissues in the head. ×50. FIG. 17. Older basidiocarp showing first external fold in the cap. ×15. FIG. 18. Section of basidiocarp of fig. 17, diagrammatically represented, and showing the first complete separation of the tissues inside the head. ×14. FIG. 19. Older basidiocarp showing progressive separation of internal tissues. Section diagrammatic with future hymenium restricted in this section to upper lobe. (Other sections show other lobes as fertile.) ×14. FIG. 20. Hymenium from fig. 19. Cross-walls are infrequent and the nuclei are in active division at this stage. ×1550. FIG. 21. Surface hyphae which comprise sterile areas of the same basidiocarp; the largest cell is a cystidium. ×1550. FIG. 22. Developing basidiocarp showing infolding on upper and lower surfaces. ×15. FIG. 23. Section of basidiocarp of approximately same age as that shown in fig. 22, with complete separation of cap and stalk tissues; the hymenium occurs on the left side and partly covers the upper surface. ×14. FIG. 24. A mature basidiocarp. ×0.75. FIG. 25. Mature basidiocarp strongly lateral in the attachment of cap and stalk. ×1.2. FIG. 26. Diagrammatic section of basidiocarp shown in fig. 24. ×47. FIG. 27. Completely matured basidiocarp with younger one connate at the base. ×2. FIG. 28. Section of a much inflated and lobed mature basidiocarp. In this section the fertile area is on the left margin but in other sections fertile areas occurred on the right lobes and not on the left. Diagrammatic. ×47. FIG. 29. Stalk hyphae with thickened walls from a mature basidiocarp. ×550. FIG. 30. Detail of subhymenium. ×937.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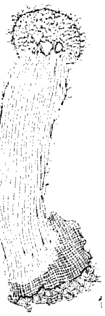
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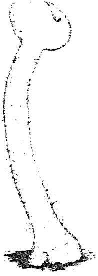
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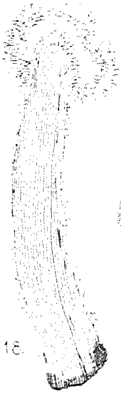
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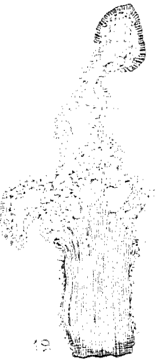
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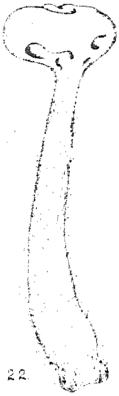
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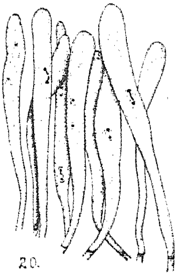
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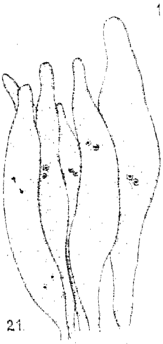
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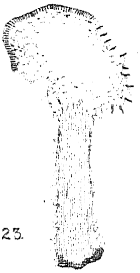
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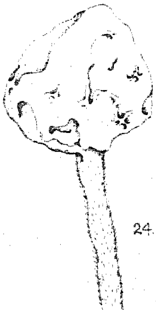
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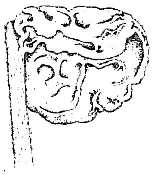
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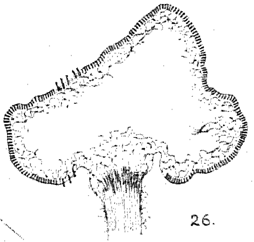
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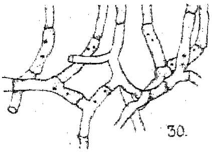
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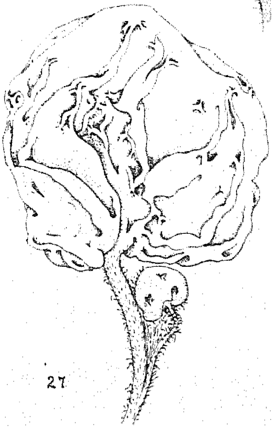
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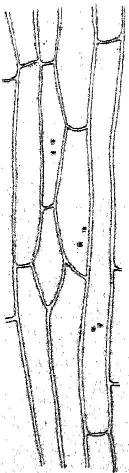
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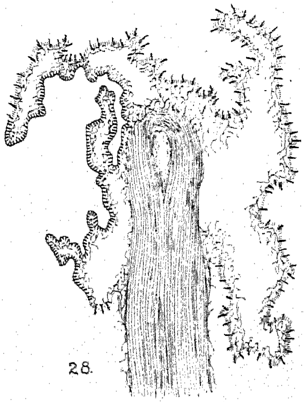
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they should be designated caulocystidia, sensu Buller, but such a distinction seems unnecessary here.

As internal differentiation progresses conspicuous openings appear in the cap immediately above the termination of the stalk hyphae (fig. 16). Later these become confluent and through more extensive growth make the first separation between cap and stalk tissues (cf. figs. 17, 18, 19). The surface hyphae are at this time approaching their ultimate size and arrangement (figs. 20, 21). The hymenium consists of closely parallel hyphae whose slender clavate tips contain dense cytoplasm and whose nuclei are either undergoing karyogamy or are in varying stages of division, presumably meiotic. The fertile hyphae are supported by a subhymenial layer of loosely interwoven cells. No mature basidia are to be found at this stage. Cross walls are infrequent, so that often two sets of nuclei appear in one hyphal end. However, the hymenial distribution is well-marked, because the sterile surface hyphae are larger, fusiform, and more vacuolate than the fertile tips. Ventricose cystidia are prominent in this tissue. Some are not emergent and their nuclei are commonly in karyogamy or in the first meiotic division. Those which do project are usually binucleate, having resulted from fusion and one division. Nuclei in both the subhymenium and the underlying reticulum of the cap are still actively dividing. Such division allows for the continued expansion and inflation of the cap.

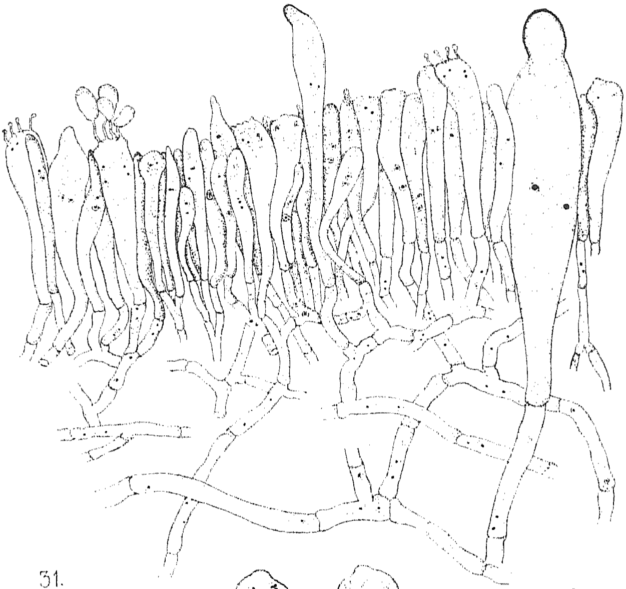
Just before the maturation of the hymenium the cap shows externally the first conspicuous folds, predominantly on the lower side, and internally the complete separation of the cap from the stalk (figs. 22, 23). Projecting cystidia of two types occur over the head: large ventricose ones which have a thickened rostrate head and slender fusiform ones which may or may not have thickened tips. They are all binucleate. Apparently these cystidia reach maturity in advance of the basidia and the surface cells of the sterile zones; the nuclei of the two latter cell-types being mostly in karyogamy or the division thereafter. Stalk and subhymenial cell nuclei are likewise often in division.

The mature basidiocarp has clearly distinct fertile and sterile surface areas. According to its age it is more or less convolute and inflated. The infoldings are due to the expansion of the cap tissues, both fertile and sterile. In section a basidiocarp of external appearance, such as that shown in figure 24, has a hymenial layer about 20 μ thick, supported by the subhymenium ranging from 10–15 μ in thickness (fig. 30), both of which are supported from below by a zone of loose reticulate hyphae from 50–150 μ deep. The sterile portions, which are from 30–40 μ thick, rest directly on the reticulum. The remainder of the cap is entirely hollow except in the region of the stalk, where the parallel hyphae may protrude into the hollow, although generally these tissues are covered by a few reticulate strands (fig. 26). The stalk tissues may be confluent with the reticulum of the cap when the lateral attachment of the stalk is extreme or the convolutions are highly irregular (figs. 25, 28). It is evident that although collapse of the bladder may explain some irregularities of the cap, the foldings are usually due to differences in expansion, for the cell layers show no signs of shrinkage or distortion.

When completely mature the basidiocarp is extremely convoluted and greatly expanded (fig. 27). The walls of the mature stalk cells are much thickened, the cytoplasmic content is reduced, but the nuclei are still prominently associated in pairs (fig. 29). The distribution of the hymenium is variable but never amphigenous. A detailed examination of the hymenium from a section of the basidiocarp illustrated in figure 24 reveals that it is composed of basidia, paraphyses, and cystidia (fig. 31). The surface of the sterile part is made up entirely of fusiform, expanded cells. Altogether four kinds of sterile elements may be distinguished in *Physalacria*. McGuire (1939), who mentions the large ventricose cystidia and smaller, slender fusiform ones, described their form and position correctly. Both occur over the entire head, but more abundantly in the sterile portions. Ventricose cystidia, which are conspicuous for their thickened rostrate heads and their enormous size (26–52 × 4–10 μ) project from 9 to 30 μ above the surface. Fusiform cystidia, 40–50 × 4–6 μ, occur freely in the sterile portions, and less frequently in the fertile tissue than the ventricose type. Furthermore, the fusiform ones are often found in greatest numbers in the transition region between fertile and sterile areas. This difference in distribution may be seen in diagrammatic representation (fig. 100). The fusiform type is further distinguished in that it projects farther, as much as 50 μ, and is always emergent. Occasionally the tip is thickened. Both kinds of cystidia are comparatively full of cytoplasm and are binucleate.

Besides the cystidia there are the cells which constitute the bulk of the sterile surface layer. These are fusiform cells of an intermediate size, 24–31 × 4–9 μ; their free ends are never thickened, however, and they are united in a compact upright layer. None of them projects beyond the surface, although, being somewhat variable in length, they form a slightly uneven surface. Their extreme vacuolation is most conspicuous and from most of them the nuclei have disappeared.

Amongst the basidia are found the much smaller paraphyses, which are also non-emergent, unencrusted cells. Figures 31 and 56 illustrate these sterile and fertile elements, drawn to a common scale. The hymenium rests on the subhymenium, which consists of small hyphae, 1–2 μ in diameter, more or less upright in position, parallel for the most part, but occasionally branched and interwoven. This layer is supported from below by the cells of the reticulum, which are coarser, 2–4 μ in diameter, and definitely intertwined. All of its cells are binucleate with irregular cytoplasmic content. The subhymenium is lacking in the sterile parts.



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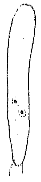

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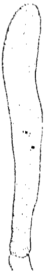

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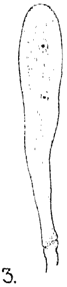

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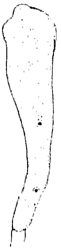

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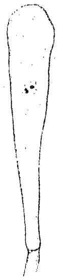

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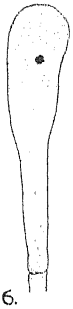

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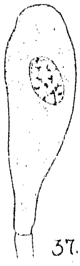

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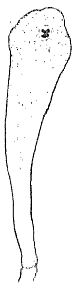

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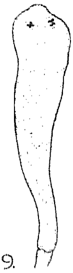

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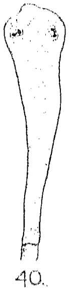

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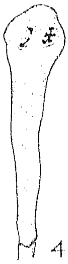

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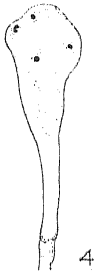

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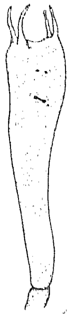

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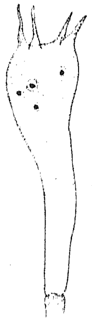

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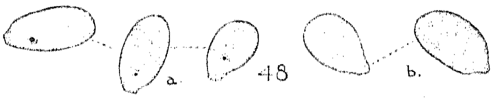

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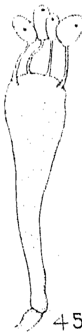

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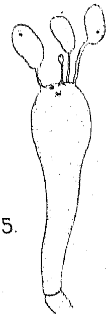

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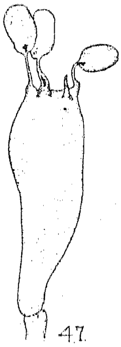

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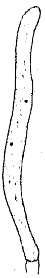

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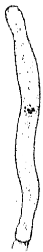

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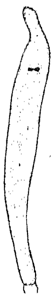

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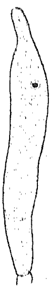

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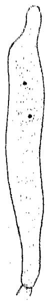

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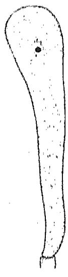

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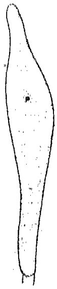

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Basidia usually arise as terminal hyphal cells, and develop in series. Consequently in any given portion of the hymenium stages of development may range from very young basidia with unfused nuclei to mature basidia which are slightly emergent at the time of spore discharge. Cytologically the development of the basidium is that any typical homobasidum. Even when very young the basidia are comparatively distinct from the paraphyses, for they are shorter and more clavate as early as the pre-fusion stage (cf. figs. 54 and 55). The young basidium is densely protoplasmic and binucleate (fig. 32). By the time nuclear fusion has taken place it has already enlarged considerably, and become slightly vacuolate. Before fusion the nuclei lie midway in the cell. As the basidium enlarges the nuclei also increase in size (fig. 33). The basidium is well on its way to maturity before karyogamy occurs (figs. 34, 35). At the time of fusion the two nuclei move near the enlarged end (fig. 36). Here fusion takes place and is soon followed by the prophase of the first division, which is probably meiotic (figs. 37, 38). The basidium continues to enlarge at the outer end. The second division follows at once (figs. 39, 40), although the division of the two daughter nuclei is not necessarily simultaneous (fig. 41). At the four-nucleate stage the basidium is decidedly enlarged and near its maximum size. The four nuclei lie toward the outer surface (fig. 42). Sterigmata then appear, growing to a length of 1 or 2 μ before the spore vesicles begin to form (figs. 43, 44). As the sterigmata and spores develop the basidium becomes correspondingly more vacuolate. The nuclei move near the sterigmata, pass through them into the spores in an attenuated mass, and finally are reorganized within the young spores

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Explanation of figures 31–55

Physalacria inflata. Fig. 31. Detail of mature hymenium, subhymenium, and a portion of the reticulate hyphae. × 1250. Fig. 32. Young basidia, pre-fusion. × 2060. Fig. 33. Older basidium, pre-fusion. × 2060. Fig. 34. Older basidium, pre-fusion. × 2060. Fig. 35. Basidium with fusing nuclei. × 2060. Fig. 36. Basidium with fusion nucleus. × 2060. Fig. 37. Basidium with nucleus in prophase of first post-fusion division. × 2060. Fig. 38. Basidium with nucleus at end of first post-fusion division. × 2060. Fig. 39. Basidium, two-nucleate, the nuclei in the second post-fusion division. × 2060. Fig. 40. Basidium with nuclei near the end of the second post-fusion division. × 2060. Fig. 41. Basidium with two nuclei in division, one nucleus in advance of the other. × 2060. Fig. 42. Four-nucleate basidium. × 2060. Fig. 43. Basidium with four sterigmata and four nuclei approaching end of second division. × 2060. Fig. 44. Basidium with four sterigmata previous to spore formation. × 2060. Fig. 45. Four-spored basidium, the spores immature. × 2060. Fig. 46. Basidium with developing spores, two nuclei still in the basidium. × 2060. Fig. 47. Basidium with three mature spores and one nucleus passing through the sterigma. × 2060. Fig. 48. *a*. Mature spores from permanent slides. × 2060. *b*. Spores from a fresh mount. × 2060. Fig. 49. Young paraphysis from fertile zone, pre-fusion. × 2060. Fig. 50. Paraphysis from fertile zone, the nuclei fusing. × 2060. Fig. 51. Paraphysis with nucleus dividing. × 2060. Fig. 52. Mature uninucleate paraphysis. × 2060. Fig. 53. Mature binucleate paraphysis. × 2060. Fig. 54. Uninucleate post-fusion basidium. × 2060. Fig. 55. Uninucleate post-fusion paraphysis from the same preparation as fig. 54, and adjacent to the basidium figured there. × 2060.

(figs. 45, 46, 47). Spore formation and nuclear migration are not always simultaneous in the same basidium (fig. 47). The spores are apparently uninucleate. In only one did two nuclei appear to be present. Peck (1882) claimed that the basidia were two-spored. Neither fresh mounts nor serial sections confirmed this statement. One basidium, already past spore-bearing, seemingly had two nuclei still in the cell, which was almost devoid of cytoplasm; one of these nuclei likewise seemed to be disintegrating. If so, it may be that when and if two-spored forms occur the extra nuclei degenerate.

In the development of the paraphyses in the hymenium it appears that their nuclei go through karyogamy, after which one division may occur, although commonly there is no further nuclear change after fusion (figs. 49–53). Mature uninucleate paraphyses are readily separable from uninucleate basidia by reason of form and size (figs. 54, 55). Fusiform cystidia usually undergo one division after fusion of their nuclei and then remain conspicuously binucleate (figs. 57–59).

The cells which comprise the sterile layer arise in the same manner as basidia: from the ends of hyphal filaments. As soon as the cap is distinguished from the stalk, but long before its tissues are mature, it is possible to recognize the hyphae which become the cells of the sterile regions and those which will become the hymenial layer. Th former are definitely larger, more fusiform, and less densely filled with cytoplasm. The sterile cells mature in advance of the basidia, as has been already pointed out. Nuclear fusion occurs here as in the cystidia and basidia and is then followed by one division (figs. 60–62). No subsequent division was noted and in mature basidiocarps these cells quite commonly have no nuclei. Since chromosomal elements are too small to distinguish as units, it is impossible to say whether the one division that follows fusion in the sterile cells is meiotic.

In any part of the fructification the ventricose-rostrate cystidia are the most striking elements. Their nuclear history is clearly defined. The nuclei of the dikaryon enlarge, come together, and thereupon the membrane breaks down at the point of contiguity (figs. 63, 64). A large fusion nucleus results which proceeds from a conspicuous prophase (fig. 65) through successive karyokinetic stages, and ends with the return of the binucleate condition (figs. 66–68). Further division does not seem to occur and the two nuclei remain more or less central in the cystidium. No indication of future disintegration was noted, although the cytoplasm becomes more vacuolate with maturity.

Obviously the variation which attends the formation of the sterile cells is more striking than the already well-known pattern of the basidium development. Cytological studies dealing with the sterile elements of the basidiomycetes are relatively few. Whelden (1936) cited what literature there is on the subject when he published an account of cystidial and gloeocystidial behavior in a species of *Peniophora*, one of the *Thelephoraceae*. Whelden traced the nuclear changes in cystidia from the fusion of the dikaryon nuclei through one division of the fusion nucleus. After this the nuclei disintegrate and later disappear completely. The development of the gloeocystidia remains obscure because of their dense content. However, gloeocystidia are definitely distinguished from cystidia because they arise as lateral branches of the deeper hyphae of the mycelium and not as hyphal tips, from which the cystidia are formed.

In *Physalacria* there are four distinct types of sterile cells, already described. Of these three types take their origin from hyphal tips: namely, the paraphyses found amongst the basidia, the projecting fusiform cystidia, and the inflated fusiform cells of the sterile tissue. Although all these have a common origin their subsequent history is not identical; but in none of them does nuclear development proceed beyond one division of the fusion nucleus. It would be interesting to know the exact nature of this division, whether it is meiotic or not, but the nuclei are too small to permit chromosome counts. The origin of the ventricose-rostrate cystidia is various. At times it is distinctly from a terminal cell, but when the cystidium remains disposed internally within the reticulum it may arise from a lateral cell. In these fusion and one division thereafter are clearly demonstrable.

The first three types of cystidia are comparable in their origin to a basidium, though morphologically they are distinct in early stages of development. Certainly the ventricose-rostrate cystidia are distinct from the beginning. Their origin, even when terminal, seems to be associated with the internal tissues and since they do not take their origin from surface cells it is likely that their primordia are not comparable to the basidial primordia. They would appear to be modified cells of the internal mycelium, some of which push through the surface layers to the outside, and some of which remain inside. Krieger (1923) referred to these ventricose cystidia as "ducts," but nothing to support this contention was observed.

As McGuire (1939) has stated, the determination of fertile and sterile areas is relatively obvious, owing to the more compact appearance of the basidial layer and the greater frequency of the projecting cystidia in the sterile parts. Twelve basidiocarps of mature differentiation were sectioned serially and compared for hymenial distribution. From these it was apparent that little if any regularity pertains to the distribution of the hymenium. McGuire found experimentally that the basidiocarps do not invariably grow erect, but the hymenium may be directed downward. In the material used here six basidiocarps had hymenium only on the lower surfaces near the stalk, and none on the upper surfaces (fig. 101). It may be assumed that these six grew more or less upright. Three had the hymenium predominantly situated on the surfaces away from the stalk. Their position might have been inverted or lateral (fig. 103). One basidiocarp had the hymenium spread irregularly over all portions of the cap, sometimes even amphigenously in single sections, though one lateral aspect was intermittently fertile, and hence may have grown slightly obliquely (fig. 102). Another basidiocarp had a hymenium so scattered in all parts that its position might have been only slightly lateral, or almost erect (fig. 105). Three connate basidiocarps displayed in section both under and upper surfaces fertile (fig. 104). To such basidiocarps McGuire's statement that the hymenium invariably "occupies the portion of the head which is actually turned downward" could not apply. It seems that the most definite conclusion one can draw is that the hymenial distribution is highly irregular and that it is never completely amphigenous over the surface of the cap, but that apparently there is a predisposition for the under surfaces to be fertile.

TAXONOMIC POSITION

Ordinarily the family *Clavariaceae* is classified between the *Thelephoraceae* and the *Hydnaceae*. As usually defined the family includes genera whose erect sporocarps are either simple or branched in varying degrees of complexity. The hymenium covers "most of the plant, usually all except a more or less well defined base or stem, which may fade imperceptibly into the upper part or be more or less delimited by a change in size or color" (Coker 1923). Nearly all taxonomic treatments summarize this diagnosis by saying briefly that the hymenium is amphigenous. If such a criterion is to be applied without any latitude, *Physalacria* will be excluded from the family.

But the confusion which has attended the understanding of the genus *Physalacria* extends to the family as a whole. Distinctions amongst the comparatively few genera included in the *Clavariaceae* (eight in Killerman 1928) are none too satisfactory. Intergrading of some genera makes their limits indeterminate, and lack of information or misunderstanding of structure of others has led to false assumptions. Genera have been set apart variously, but chiefly on differences in form and texture of the basidiocarp; distribution of the hymenium; distinctions of head and stalk regions; presence or absence of sclerotia; and the number of spores borne by the basidia. These lines of segregation fail to separate all genera distinctly. As a result some forms have been shifted to other families and even new families erected to satisfy variations.

For example, Remsberg (1940) has pointed out the confusion existing between *Typhula* and *Pistillaria*, when the distinction between them relies on body form or texture. The presence of a sclerotium in *Typhula* she finds the only good single morphological criterion which is consistently reliable, although the presence of a swollen hymenial portion, the clavula, would seem to be concomitant. Except for this definite character, representatives of

Pistillaria or *Clavaria* might with equal warrant be referred to the genus *Typhula*.

Numbers of spores have not proved good criteria, as witness the claim often advanced that *Pistillaria* basidia are two-spored whereas those of *Typhula* are four-spored (Killerman 1928, Bessey 1935). The fallacy of relying upon such a distinction is clear when one consults Remsberg's work, which showed that two- and four-spored basidia occur freely in typical species of the same genus, and one species is six- or eight-spored. Nor is such variability limited to *Typhula*. Amongst the species of *Physalacria* observed some are consistently two-spored, others are consistently four-spored, and again, in the same species and more particularly in the same basidiocarp, both two- and four-spored basidia occur. Furthermore, in *Clavaria*, defined as a two- or four-spored form, some species have six and eight spores. This would explain Wakyama's statement that the *Clavaria* basidium has eight nuclei; in all probability he had an eight-spored form. No *Clavaria* basidium of the four-spored type has been noted with more than four nuclei.

The question of distribution and position of the hymenium has led to various changes in the family. If only those forms which are distinctly amphigenous are to be regarded as *Clavariaceae*, those genera, of which there are several, whose hymenial distribution is scattered will have to be classified elsewhere. Several such redistributions have been suggested. Krieger (1923), struck by the superficial resemblance of the under lobes of *Physalacria inflata* to the gills of agarics, proposed to move *Physalacria* into a new, transitional family, the *Eoagaricaceae*. Coker (1923) misled by this precipitate judgment, followed Krieger's suggestion and consequently failed to recognize the genus amongst the *Clavariaceae*. McGuire (1939) pointed out that the fertile parts of *Physalacria* were not necessarily on the under side, as Krieger thought, but because they seemed to be unilateral he advocated classifying the genus with the *Thelephoraceae*. Similarly *Sparassis* has been transferred to the *Thelephoraceae* because its hymenium occupies the under sides of the lobes (Cotton 1912), with which assignment Coker (1923) concurs. Sterile lines and areas here and there over the surface of *Clavaria* have long been accepted (Coker 1923), particularly in the forks, though apparently there is no known relationship between the distribution of the hymenium and its position. Clavarias have been found with not only scattered hymenial areas but some blunt projecting cystidial cells. Just as in *Physalacria*, fertile and sterile areas may be recognized by their denser palisade layers. In two species examined these areas were quite distinct, somewhat scattered, and the fertile layer tapered off gradually at the stalk. This returns the question then to the amphigenous nature of the basidiocarp. On that basis *Physalacria* can only be removed if all other forms without completely amphigenous hymenia are removed too.

In the light of the foregoing remarks it would appear that it would be more feasible first to establish limits for the family *Clavariaceae* that are broad enough to include these variations, rather than to scatter too widely those forms which show basic relationships. When more critical knowledge is accumulated for the different genera, re-arrangements and transfers may be in order. For the present any transfer of *Physalacria* from the *Clavariaceae* would seem entirely unnecessary as well as untenable.

In reviewing the published descriptions of already established species of *Physalacria*, a fairly large number is found, thirteen, some of which do not appear to be valid. Of the total only three have been reported from United States. The majority of the remainder are from various parts of the tropics. In addition to previously described forms, specimens collected by G. W. Martin in Panama and Colombia seem to be distinct. Inasmuch as it was impossible to see representatives of all described species, any treatment of the genus as a whole must be tentative. However, since no comprehensive study of the genus exists, descriptions of species seen may prove useful, and a provisional key based in part on publications may serve until such time as more specimens can be critically studied.

KEY TO THE SPECIES

1. Basidiocarps predominantly globular, rugose, hollow .... 2.
1. Basidiocarps conical, usually small, smooth or rugose, hollow .... 10.
    2. Basidiocarps yellow or pale ochraceous .... 3.
    2. Basidiocarps white or cream colored, often pruinose .... 4.
3. Spores elongate-elliptical, 13–17 × 2.5–3 µ .... *P. Clusiae.*
3. Spores oval, 4 × 3 µ .... *P. stilboidea.*
    4. Basidiocarps large, over 1 mm. in diam. .... 5.
    4. Basidiocarps small, under 1 mm. in diam. .... 7.
5. Basidia typically four-spored .... *P. inflata.*
5. Basidia two- or four-spored .... 6.
    6. Spores ovoid-elliptical, 6–7 × 3.5–4.5 µ .... *P. orinocensis.*
    6. Spores ovoid to subglobose, 4.5–6.0 × 3–3.5 µ .... *P. aggregata.*
7. Cystidia lacking, spores roughened .... *P. Bambusae.*
7. Cystidia present .... 8.
    8. Cystidia conical, flask-shaped, 30 × 8 µ .... *P. villosa.*
    8. Cystidia chiefly ventricose-rostrate .... 9.
9. Cystidia infrequent, 22–35 × 5–15 µ .... *P. Langloisii.*
9. Cystidia with conspicuous red-brown resinous heads, 70 × 6–8 (–10) µ .... *P. concinna.*
    10. Basidia four-spored .... *P. Decaryi.*
    10. Basidia two-spored .... 11.
11. Spores 7–10 × 4–5.5 µ .... *P. andina.*
11. Spores smaller, ovoid-elliptical to pyriform, 3.1–4 × 1.5–2 µ .... *P. Sanctae-Martae.*

PHYSALACRIA CLUSIAE Syd. Ann. Myc. **28**: 35. 1930. Fig. 76.

Basidiocarps globose, or slightly depressed-globose, the hymenium amphigenous; growing over areas measuring 1.4 cm., clustered or not, ochraceous-yellow; stipes short, 150–220 µ long, 80–140 µ in diam.; hyphae 2–4 µ thick, irregular, rigid and parallel in the stipe; cystidia more or less prominent, clavate or cylindrical-clavate, 20–50 × 10–20 μ, sometimes possessing an oily-resinous head; cystidia in the stipe short and with a thick covering; basidia clavate, 25–30 μ, sterigmata 2–4(–10) μ long; spores more or less distinctly fusoid, directly or slightly unequal, the apex gradually attenuated, the base abruptly attenuated, possessing a few or numerous minute guttules, continuous, hyaline, 13–17 × 2.5–3 μ.

The only representative of this species seen was so immature that critical characters could not be checked. The description is taken from that of Sydow. Described from Venezuela.

VENEZUELA: Puerto La Cruz, Dec. 30, 1927, Sydow, 760, TYPE (in Farlow Herb.).

PHYSALACRIA STILBOIDEA (Cooke) Sacc. Syll. Fung. 9: 256. 1891. *Pistillina stilboidea* Cooke, Grev. 19: 2. 1890.

From the description of this fungus in Saccardo, it appears to be characterized by fleshy, gregarious basidiocarps, pale ochraceous, stipitate, erect, capitate, minute, scarcely 3 mm. high; the head is globose-depressed or globular, hollow, hymeniferous, 0.25–1 mm. in diam.; stipe cylindrical, equal, solid, pruinose, 1.5 mm. long, expanded at the base; basidia cylindrico-clavate, hyaline; spores hyaline, 4 × 3 μ.

Described from New Zealand. No specimens were available for study.

PHYSALACRIA INFLATA (Schw.) Peck, Bull. Torr. Club 9: 2. 1882. *Mitrula inflata* Schw. in Fries' *Elenchus Fungorum* 1: 234–235. 1828. *Eoagaricus inflatus* (Schw.) Kr. Md. Acad. Sci. 3: 8. 1923. Figs. 1–68.

Basidiocarps gregarious, sometimes confluent, or scattered, white, capitate, globose to subglobose, much folded at maturity, hollow, up to a few cm. in diam.; borne on a distinct stalk, centrally or laterally attached, solid, tapering from base to apex, often pruinose from projecting cystidia; hymenium occurring only in restricted areas over the surface of the head, commonly on the side directed downward; cystidia of various form: ventricose-rostrate 26–52 × 4–10 μ, projecting above the surface as much as 30 μ; fusiform cystidia abundant in the sterile areas, less common in the fertile tissue, 40–50 × 4–6 μ, the tip occasionally thickened, projecting up to 50 μ; paraphyses amongst the basidia non-emergent, unencrusted, 27–31 × 2–3 μ; basidia four-spored, 15–18 × 4–5.5 μ; spores hyaline, uninucleate, ovoid-elliptical, 4–6 × 2.5–3.5 μ; growing on dead wood or leaves.

CANADA: Ontario, Aurora, Sept. 25, 1934, *R. F. Cain 3250;* London, Oct. 26, 1889, *Dearness*, ex Ellis Coll., 980 (in Herb. N. Y. Bot. Gard.); Ontario, Magnetwan, Sept. 1921, *L. C. C. Krieger 1310* (in Herb. Univ. Mich.). UNITED STATES—PENNSYLVANIA: Keshan Fall; NEW HAMPSHIRE: Shelburne, June 1888, *Farlow*, ex Ellis Coll.; MARYLAND: Aug. 5, 1891, *Sturgis;* (in Herb. N. Y. Bot. Gard.); WISCONSIN: Door County, Jacksonport, July 25, 27, 1935, *Baker 124;* NEBRASKA: *DeWitt*, June 12, 1938, *J. M. McGuire* (in Herb. Univ. Iowa).

PHYSALACRIA ORINOCENSIS Pat. and Gaill. Bull. Soc. Myc. Fr. 4: 41. 1888. Figs. 77–82.

Basidiocarps globose, fairly smooth when young, becoming lobed and gyrose with age; white to cream to buff when dry, 0.58–1.6 × 0.55–2 mm., borne on straight or slightly curved, slender stalks, 0.55–0.75(–3.5) mm., sometimes expanded basally, but not projecting far within the head, and terminating there in a few uneven strands; hymenium not amphigenous, 15–24 μ thick; subhymenium scant, rather coarse, about 10 μ thick, resting on a thin layer of reticulate hyphae; cystidia numerous, ventricose-rostrate, often quite large and conspicuously encrusted; smaller fusiform and unencrusted cystidia, not projecting, 12–13 × 3 μ; basidia four- or two-spored, 18–22 × 4–5 μ, sterigmata (2–)3–3.5 μ long; spores ovoid-elliptical, sometimes flattened slightly on one side, laterally apiculate, rarely guttulate, 6–7.5 × 3.5–4.5 μ.

VENEZUELA: July 1887, *Patouillard 81*, TYPE (in Farlow Herb.). PHILIPPINE ISLANDS: Luzon, Mt. Maquiling, Oct. 1920, *Reinking 10034* (in Farlow Herb.). FRENCH INDO-CHINA: Tonkin, Ke So, April 6, 1891, *Bon 4696* (in Farlow Herb.); Hanoi, *Demange 299*, ex Herb. Pat., 1858 (in Farlow Herb.).

Physalacria aggregata Martin and Baker, sp. nov. Figs. 88–93.

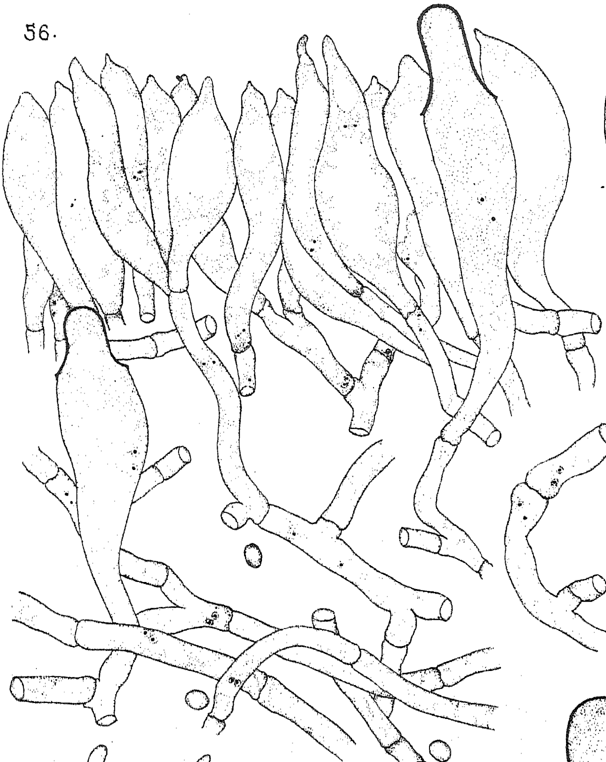
Gregaria vel conferta; capitulum subglobosum vel ellipsoideum, lobatum, cavum, album, sicco ochraceum, 0.5–2.4 × 0.4–1.1 mm.; stipes tenuis, 0.9–1.8 mm. altus; cystidiis duplicibus, ventricosis, rostratis, 50–54 × 9–12 μ, et fusiformibus, incrustatis, 50 × 10 μ; basidiis 4-sporis, raro 2-sporis; basidiosporis ovoideis vel subglobosis, 3.5–6 × 2–3.5 μ.

Basidiocarps more or less spherical, somewhat irregular, lobed, 0.5–1.2–2.4 × 0.4–1.1 mm.; white when young, drying ochraceous; stalks slender, mostly central, 0.9–1.8 mm. high; the head hollow, the stalk projecting slightly into the cavity, ending in a few scattered strands of hyphae; hymenium distributed irregularly over the surface, from 10–15 μ thick, resting on a compact layer about 10–13 μ thick, composed of rather fine, interwoven hyphae; stalk of parallel hyphae which arise from a basal zone of pseudo-parenchyma and terminate in the head in a compact anastomosed mass, not strictly pseudo-parenchymatous as in *P. andina*, finally dissipating in a few strands passing outwards to the margin; cystidia of the ventricose-rostrate type 50–54 × 9–12 μ, originating well below the hymenium and projecting about 8–10 μ; encrusted cystidia 50 × 10 μ; paraphyses in the hymenium 22 × 3 μ; basidia (10–)12–14 × 2.5–4 μ, four-spored, rarely two-spored; sterigmata about 3 μ long; spores ovoid and flattened on one side to subglobose, with a definite lateral apiculus, rarely somewhat reniform (3.5–)4.5–6.0 × (2–)3–3.5 μ.

PANAMA: Chiriquí, Valley of upper Rio Chiriquí Viejo, July 1, 1935, *G. W. Martin 2260, 2261*, TYPE, *2321, 2321a, 2586* (in Herb. Univ. Iowa).

Explanation of figures 56–68.

Physalacria inflata. FIG. 56. Detail of sterile surface cells, including two ventricose-rostrate cystidia. × 1250. FIG. 57. Young fusiform cystidium, pre-fusion, from sterile surface of the head, the surface level marked. × 1250. FIG. 58. Nuclei dividing in a cystidium from the margin of a stalk. × 1250. FIG. 59. Pre-fusion, two-nucleate cystidium from surface of the stalk. × 1250. FIG. 60. Sterile cell from sterile zone with the nuclei fusing. × 2060. FIG. 61. Sterile cell from sterile zone, the post-fusion nucleus dividing. × 2060. FIG. 62. Division of the post-fusion nucleus in a sterile surface cell. × 2060. FIG. 63. Ventricose-rostrate cystidium, two-nucleate, and pre-fusion. × 2060. FIG. 64. Fusion of nuclei in ventricose-rostrate cystidium. × 2060. FIG. 65. Prophase of post-fusion division in ventricose-rostrate cystidium. × 2060. FIG. 66. First division of fusion nucleus of ventricose-rostrate cystidium. × 2060. FIGS. 67, 68. End of the first division in the ventricose-rostrate cystidia. × 2060.



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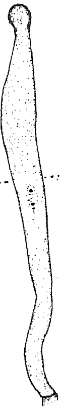

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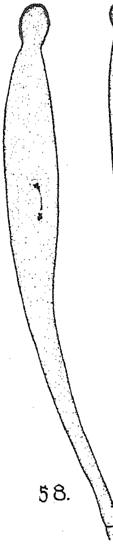

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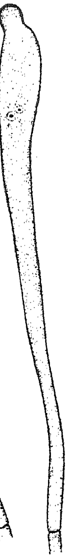

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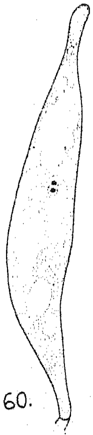

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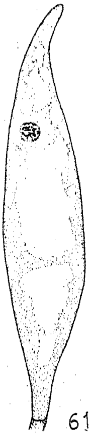

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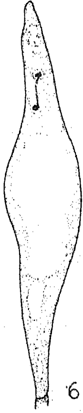

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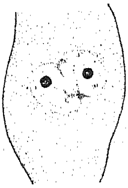

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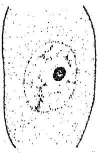

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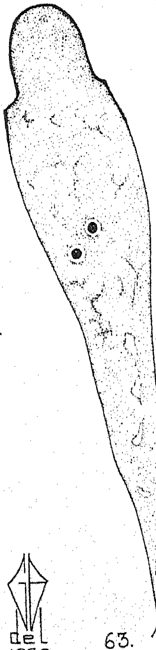

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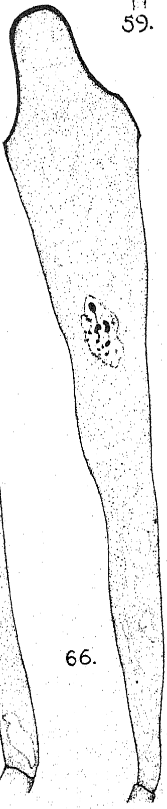

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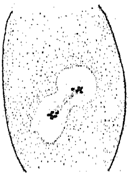

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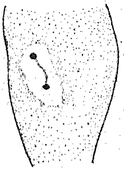

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1939.

PHYSALACRIA BAMBUSAE von Höhnel, Sitz.-ber. Akad. Wiss. Wien. **118**: 290. 1909.

No material of this species was seen. According to the published description the gregarious basidiocarps are from white to somewhat yellowish when dry, with heads up to 330 μ broad, vesicular, hollow, globular or ovoid, tapering when dry; stipe solid, cylindrical, of thin parallel or irregular hyphae 3–5 μ thick, 360–450 × 40–60 μ; cystidia lacking; basidia 12–14 × 3–4 μ with 4 awl-shaped sterigmata, 5 μ long; spores hyaline, globose, finely roughened, 3–4 μ across; on dead bamboo canes. Described from Java.

The lack of cystidia and the faintly roughened spores should distinguish this species clearly.

PHYSALACRIA VILLOSA Petch, Ann. Roy. Gard. Peradeniya **6**: 206. 1917.

Since no material of this form was available, Petch's account is given in brief. Basidiocarps white, heads globose, up to 0.4 mm. in diam.; stalk up to 0.7 mm. high, tapering from base to apex, 0.1 mm.–40 μ respectively, twisted above, fibrous, rough, with minute crystals and covered with cystidia, 30 × 8 μ, thick-walled, sometimes sub-capitate; basidia four-spored; on dead leaves. From Ceylon.

PHYSALACRIA CONCINNA Syd. Ann. Myc. **28**: 36. 1930.

Basidiocarps solitary or gregarious, white or yellowish-white; stipes very short, 140–180 μ high, 200 μ wide; head globular or subglobose, collapsing in the center when dry, very finely farinose, 350–600 μ diam.; hyphae 1–3 μ thick; cystidia scattered, clavate or cylindrical-clavate, up to 70 μ long, 6–8(–10) μ wide, sometimes capitate, often red-brown, oily, resinous; 12–15 μ in diam.; basidia clavate, 18–22 × 5.1–6.5 μ, 2 or 4 sterigmate; sterigmata 3–5 μ long; smaller cystidia abundant among the basidia, acute, up to 28 μ long; 5–6 μ wide in the mid-region; spores oblique-oval, apex a little attenu-

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Explanation of figures 69–99

Physalacria andina. FIG. 69. Habit sketch of basidiocarps, from *Martin 3489.* × 14. FIG. 70. Longitudinal section, diagrammatic, through a basidiocarp from *Martin 3489.* × 30. FIG. 71. Basidia from type material. × 937. FIG. 72. Spores from the type material. × 937. FIG. 73. Spores from *Martin 3489.* × 937. FIG. 74. Detail of pseudo-parenchyma at top of stalk inside cap of a basidiocarp from *Martin 3489.* × 450. FIG. 75. Cystidia from type material, the surface marked. × 937.

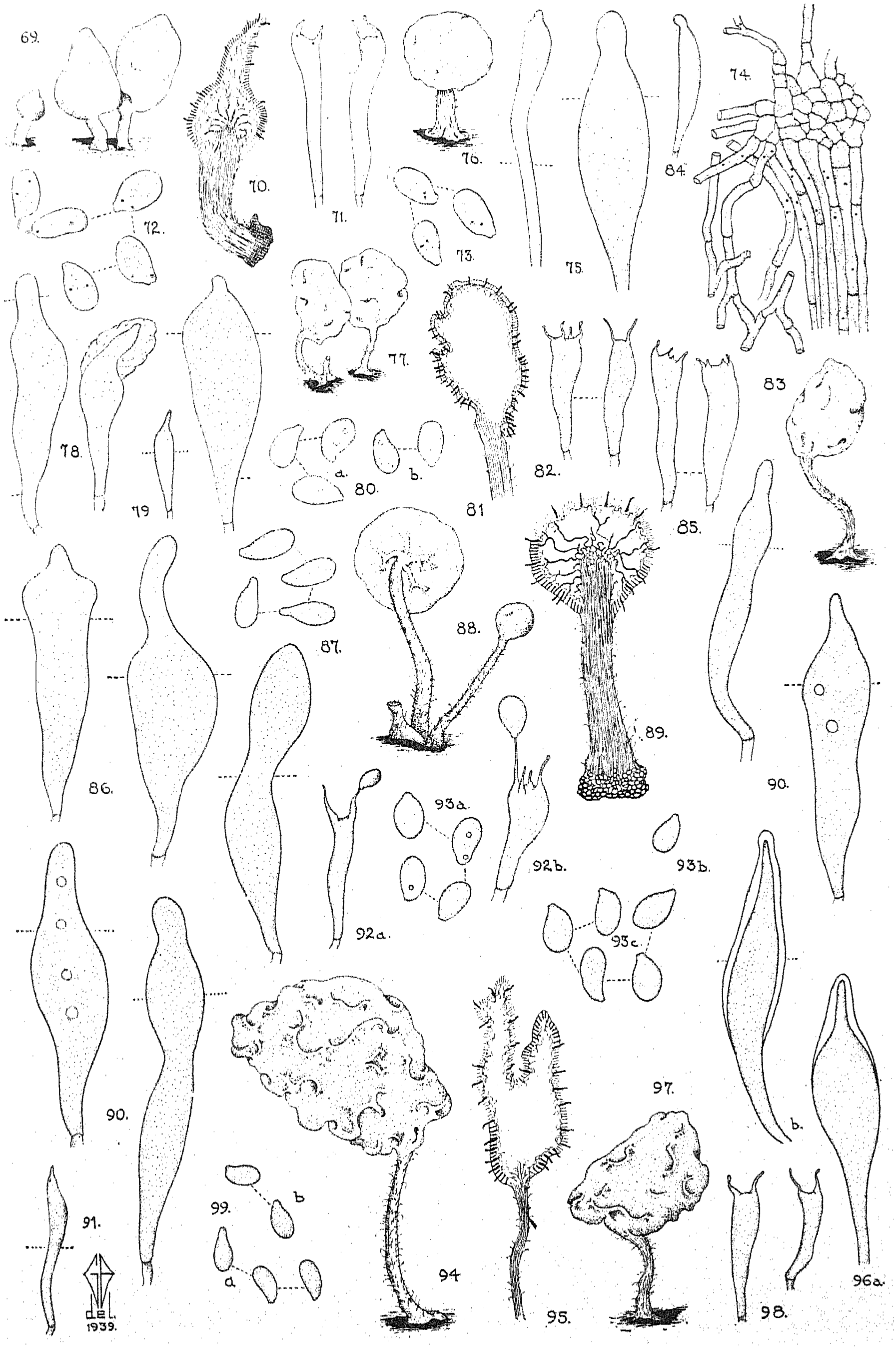
Physalacria Clusiae. FIG. 76. Habit sketch, type material. × 10.

Physalacria orinocensis. FIG. 77. Habit sketch, 4696. × 14. FIG. 78. Three cystidia from 10034 and 4696. × 937. FIG. 79. Paraphysis from hymenium, 4696. × 937. FIG. 80. *a.* Spores from 299. × 937. *b.* Spores from 10034. × 937. FIG. 81. Diagram of internal structure from a section of 10034. × 35. FIG. 82. Basidia, 299. × 1550.

Physalacria Langloisii. FIG. 83. Habit sketch, 91. × 14. FIG. 84. Paraphysis from type. × 1550. FIG. 85. Basidia from type. × 1550. FIG. 86. Cystidia from type. × 1550. FIG. 87. Spores from type. × 1550.

Physalacria aggregata. FIG. 88. Habit sketch, 2261. × 14. FIG. 89. Diagram of section, 2261. × 47. FIG. 90. Cystidia from 2261. × 937. FIG. 91. Paraphysis from hymenium of 2321. × 937. FIG. 92. *a.* Basidium, 2321. × 1550. *b.* Basidia, 2261. × 1550. FIG. 93. *a.* Spores, 2231. × 1550. *b.* Spores, 2260. × 1550. *c.* Spores, 2261. × 1550.

Physalacria Sanctae-Martae. FIG. 94. Habit sketch, 3654. × 14. FIG. 95. Diagram of longitudinal section, 3654. × 14. FIG. 96. *a.* Cystidium, 3485. × 937. *b.* Cystidium, 3654. × 937. FIG. 97. Habit sketch, 3485. × 14. FIG. 98. Basidia, 3654. × 1550. FIG. 99. *a.* Spores, 3654. × 1550. *b.* Spores, 3704. × 1550.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ated, the base rounded, minutely apiculate, apiculus unilateral, 6–8 × 3.0–3.5 μ, continuous, hyaline. Described from Venezuela.

No examples were seen. The foregoing is taken from Sydow's account.

PHYSALACRIA LANGLOISII Ellis and Everhart, Jour. Myc. **4**: 73. 1888. Figs. 83–87.

This species, originally described from the southern United States, is now more widely distributed. Basidiocarps white or slightly yellowish, with heads from subglobose to somewhat attenuated or depressed above, becoming hollow at maturity, 0.25–1 mm. in diam.; stalk fibrous, slightly pubescent, 0.3–1 mm. or more long, usually very long in proportion to the whole basidiocarp; surface of the head not amphigenous; cystidia 22–28 × 5–7.5 μ, projecting 7–13 μ above the surface, (according to Ellis and Everhart the cystidia are 30–33 × 15 μ), clavate, often with a median constriction, or ventricose-rostrate, but never very abundant; paraphyses with the basidia more or less fusiform, 12 × 2 μ; basidia 11–13 × 2.5–3 μ (Ellis and Everhart say 12 × 2.5–3 μ); four-spored, sterigmata short; spores ovoid-elliptical, sometimes flattened on one side, or more rarely a little reniform; apiculus unilateral, 4.2–5 × 1.5–2 μ (Ellis and Everhart say 4.5 × 2–2.5 μ).

UNITED STATES—LOUISIANA: *Langlois*, TYPE, ex Herb. Ellis, (in Farlow Herb.). FLORIDA: Coconut Grove, *Thaxter 91* (in Farlow Herb.).

PHYSALACRIA DECARYI Pat. Mém. Acad. Malgache **6**: 10. 1927.

Basidiocarps entirely white, on decaying wood, in small tufts 3–4 mm. in extent; heads cylindrical, truncated at the top, hollow, attaining a height of 1 mm.; cystidia hyaline, projecting, 25 × 9–10 μ, with an apical beak; spores hyaline, ovoid, 3–4 μ; stipe slender, 150–200 μ thick, bearing cystidia which are 45 × 12–15 μ, also ending in a beak.

The author's description is drawn upon for the preceding account. In addition he remarks that this species is very closely related to *P. andina* and *P. orinocensis*, but that it is distinguished by its cylindrical form with the truncated summit and by the beaked cystidia. No specimens were obtained for examination. Described from Madagascar.

PHYSALACRIA ANDINA Pat. Essai Taxonomique, 50. 1900. *Physalacria orinocensis* var. *andina* Pat. and G. de Lagerheim, Soc. Myc. Fr. Bull. **9**: 136. 1893. *Physalacria tenera* Syd. Ann. Myc. **28**: 33. 1930. Figs. 69–75.

Two specimens from Patouillard's herbarium were examined, one of which was the type. Examinations were made in a lacto-phenol preparation, in addition to which one basidiocarp was imbedded and sectioned in paraffin. The typical *P. andina* basidiocarp is from definitely conical to acuminate

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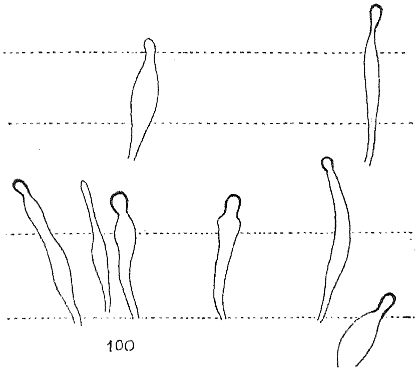
Explanation of figures 100–105

Physalacria inflata. FIG. 100. Diagrams showing distribution and frequency of large projecting cystidia in sterile (upper) and fertile (lower) surfaces with the surface level and limit of hymenial layer marked with dotted lines. Areas equivalent in extent. × 550. FIG. 101. Diagram of basidiocarp showing hymenial distribution limited to the lower surface. Fertile areas represented by dotted lines. × 15. FIG. 102. Diagram of basidiocarp with irregularly distributed hymenium, at times practically amphigenous in its surface distribution. × 15. FIG. 103. Diagram of basidiocarp showing hymenial distribution on surfaces away from the stalk region. × 15. FIG. 104. Diagrammatic view of three connate basidiocarps with hymenial surfaces on both under and upper sides. × 7.5. FIG. 105. Diagram of basidiocarp with very irregular hymenial distribution. × 15.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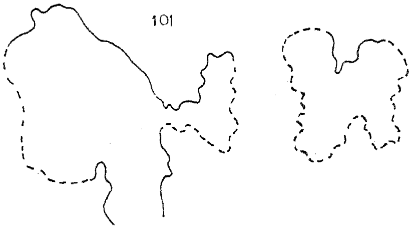
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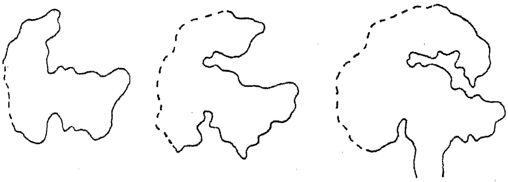
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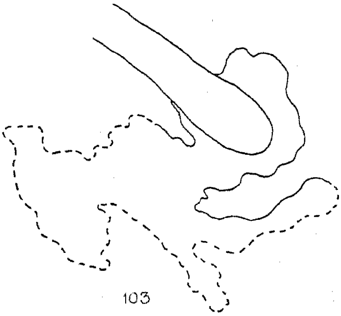
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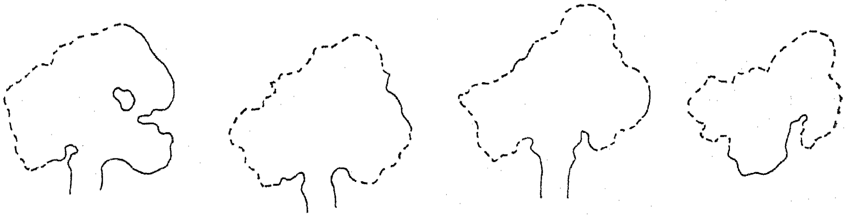

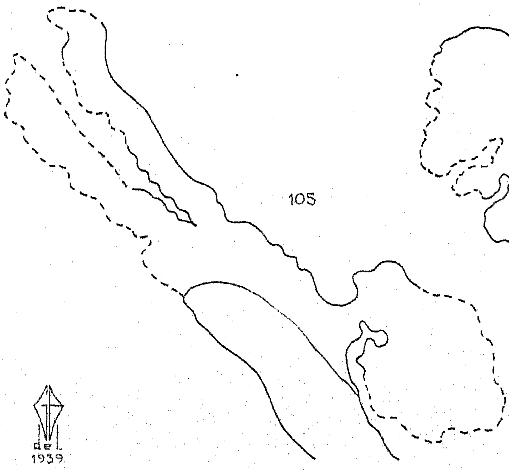
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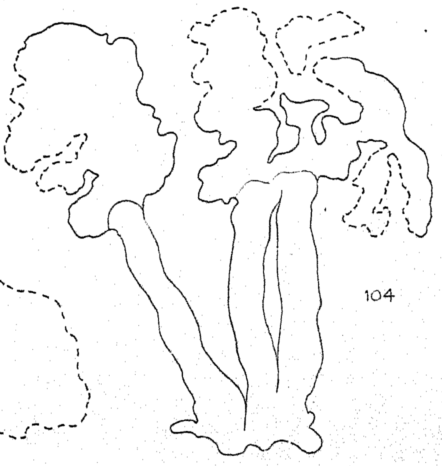
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from the very beginning and only rarely is the head curved or flexuous, 1–3.5 mm. high, 0.3–2 mm. across; stalk relatively short at maturity, 0.3–0.75 mm.; expanded head 1–2.4 × 0.35–1.2 mm.; surface smooth or slightly rugose, white to deep cream when moistened, appearing decidedly farinose; hollow, but the entire cavity penetrated by sturdy hyphae radiating from the pseudoparenchymatous end of the stipe which extends about 100–300 μ inside the head; stalk hyphae compact, parallel in arrangement, with somewhat thickened walls, binucleate cells; not amphigenous, the surface distinguished by definite fertile and sterile parts; fertile area composed of hymenium, 25–30 μ thick; subhymenium, 15–20 μ thick, poorly defined; and a basal reticulum which connects with the strands from the stalk; cystidia chiefly ventricose-rostrate, 30–40 × 12–15 μ, projecting 15–22 μ above the surface; basidia consistently bispored, (20–)22–24 × 4–5 μ, sterigmata about 3 μ long; spores from ovoid to subglobose with a definite apiculus, binucleate, 7–10 × 4–4.5 μ.

Because of the dried condition of the material when fixed, no satisfactory evidence of nuclear behavior in the basidium could be obtained. Presumably the basidia are four-nucleate and two nuclei move into each spore, for no division figures in the spores were in evidence at all.

P. tenera Syd. is here regarded as the same as *P. andina* Pat. Certainly the material examined gave no justification for maintaining the former as a separate species. The basidiocarps measured 0.75–1.2 mm. × 0.5–0.8 mm., with stalks 0.4–0.75 mm. in height. These measurements are a little under those which Sydow gives (0.75–1.5, rarely 2 mm., with stalks 0.4–1.4 mm.), and both sets of measures are under those of *P. andina*. In section there is no critical difference between them, however. Cystidia range from 40–50 μ and project for 15–25 μ. The basidia, bispored, are 23–29 × 4–4.5 μ (Sydow quotes 20–25 × 5–6 μ); spores 7–10 × 4–5.5 μ; Sydow says 6–11(–12) × 2.5–3.5(–4).

A collection from Colombia, *Martin 3489*, is undoubtedly to be included with the foregoing. The basidiocarps, typically conical, measure 0.8–1.2 × 0.4–0.6 mm., with stalks 0.3–0.5 mm. Their appearance in section is the same as the preceding forms. The basidia, bispored, range from 20 to 22 × 4.5 μ; the spores are bi-nucleate, (5.5–)8–9 × 3.5–4.5 μ. The variations in size amongst these basidiocarps and their basidia and spores is not excessive enough to be significant. The similarity of the internal structure in all three leaves little doubt that they cannot be separated.

ECUADOR: Pululahua, Feb. 1892, *de Lagerheim*, TYPE (in Farlow Herb.); March 1892, *de Lagerheim* (in Farlow Herb.); inter El Limon et Colonia Tovar, Jan. 19, 1928, *H. Sydow 759* (in Farlow Herb.). COLOMBIA—MAGDALENA: Sierra Nevada de Santa Marta, Hacienda Cincinnati, Aug. 18, 1935, *G. W. Martin 3489* (in Herb. Univ. Iowa).

Physalacria Sanctae-Martae Martin and Baker, sp. nov. Figs. 94–99.

Gregaria; capitulum ellipsoideum vel conicum, cavum, album, siccum sature ochraceum; stipes tenuis, 0.8–1.6(–5) mm. altus; cystidiis fusiformibus, parietibus supra crassis, 35–46 × 8–10 μ; basidiis 2-sporis; basidiosporis ovoideis vel piriformibus, 3.1–4 × 1.5–2 μ.

Basidiocarps well developed, ellipsoidal to somewhat conical, pure white, with conspicuous infoldings, 1.4–2.5 × 0.8–1.5 mm., supported by a slender, centrally attached stalk, 0.8–1.6(–5) mm.; pendent; hymenium not amphigenous, 10–15 μ thick; subhymenium slight, about 5 μ, resting on a reticulum 40–45 μ thick; cap entirely hollow, the stalk ending abruptly, in a manner similar to that of *P. inflata;* cystidia not prominently beaked, tapering markedly, the surface thickened for approximately one-third the length, 35–46 × 8–10 μ, projecting about 12 μ; basidia two-spored with slender sterigmata, 10–12 × 1.5–3 μ; spores small, ovoid-elliptical to pyriform, apiculus lateral, 3.1–4 × 1.5–2 μ.

COLOMBIA—MAGDALENA: Sierra Nevada de Santa Marta, Hacienda Cincinnati, Aug. 18, 1935, *G. W. Martin 3485*, TYPE (in Herb. Univ. Iowa); Cerro Quemado Trail, Aug. 23, 1935, *G. W. Martin 3654, 3704* (in Herb. Univ. Iowa).

SPECIES EXCLUDENDAE

Physalacria rugosa Rick, Broteria **5**: 12. 1906. This species is described as represented by basidiocarps nearly 0.5 mm. in diam., hemispherical, fleshy to somewhat waxy, rugose, stalk pruinose; basidia clavate, 25 μ, sterigmata 3–6 μ long; spores 3.5 × 2 μ, subhyaline; on wood. Described from Brazil.

Lloyd remarks (17) "there has been recently a species (*Physalacria rugosa*) named from Brazil, which I judge from the description is the same as our United States' species."

Two collections of Rick's purporting to be this species were examined but neither proved to be a *Physalacria.* Until authentic material is found it had best be assumed that the species is not a good one.

BRAZIL: Saõ Leopoldo, Rio Grande do Sul, 1929, *Rick;* 1928, *Rick*, ex Herb. F. Theissen, (in Farlow Herb.).

Physalacria solida F. E. and S. E. Clements, Exsicc. Colo. Fungi. The specimen seen did not present typical physalacrian characters, in particular the basidia, which were apparently a heterobasidial type. For this reason it must be excluded from the genus.

UNITED STATES—COLORADO: Minnehaha, Sept. 7, 1906, *F. E. S. S. E. Clements 333* (in Farlow Herb.).

SPECIES DUBIA

Physalacria changensis Rost. in Sacc. Syll. **17**: 203.

The author wishes to acknowledge her indebtedness to the staff of the botany department of Columbia University for placing the full facilities of the department at her disposal during the preparation of this paper, and in particular to Professor J. S. Karling for the reading of the manuscript; to Professor G. W. Martin of the University of Iowa for his tropical collections, the naming of the new species, and his continued counsel; and to the Farlow Herbarium of Harvard University for the use of the library and herbarium.

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POUGHKEEPSIE, NEW YORK

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PAPULASPORA GLADIOLI

B. O. Dodge and Thomas Laskaris

(WITH TWO FIGURES)

Much work has been done during the past thirty or forty years on corm diseases of gladiolus. When the complete story is not yet known there is bound to be some confusion regarding those symptoms which can be used to distinguish rots due to particular organisms or agents. Paragraphs with practically identical wording have been published to describe certain phases in corm diseases which were claimed at times to be due to three entirely different fungi. If one compares lists of symptoms given by various authors characterizing scab, heart rot, dry rot, and *Fusarium* rot, he will see the need for a much more careful study of all corm diseases to determine whether the same disease conditions may not be due to different sets of organisms or agents at different times and under different environmental conditions. Not enough attention is given to the work of bulb mites, thrips, and other organisms, which pave the way for invasion by fungi that may be at most only weak parasites, so that one attributes the disease to a certain species at one time and to some other species at another time.

Under the title "The 'smut' disease of *Gladiolus*," the writers (1941a) have pointed out that there is evidence that the fungus which all previous authors, including Wernham (1938) and Zundel (1939) in America, have assumed to be a true smut fungus, *Urocystis Gladioli*, is merely the *Papulaspora* stage of some other fungus, probably an Ascomycete; at least it is not a smut at all. We have found the fungus at various times on about 20 per cent of diseased corms (fig. 1 A) in collections made from a commercial storage house. A core-rot disease caused by a *Sclerotinia* (*Botrytis*) is being further discussed in another paper now in press (1941b). It is true that there is a great similarity between the bulbils of certain species of *Papulaspora* and the spore-balls of a *Urocystis*. Figure 2 B, C, shows two bulbils of the gladiolus fungus.

The method of origin of a spore-ball of *U. Colchici*, as figured by Winter (1876), is much like what one sees in a young culture of our *Papulaspora*. While a few smut fungi have been induced to complete their life cycle, forming chlamydospores in culture, it requires special methods of culture and a long time for the smut to reach maturity. This *Papulaspora* produces its bulbils (fig. 1 B, C) in great numbers within a week's time. Each fertile cell of a *Urocystis* spore-ball theoretically contains two haploid nuclei at first, and these fuse at the maturity of the spore. The central cells of a bulbil of this *Papulaspora* are multinucleate, as is readily shown in cytological preparations. The lighter colored boundary cells also contain three or four, or

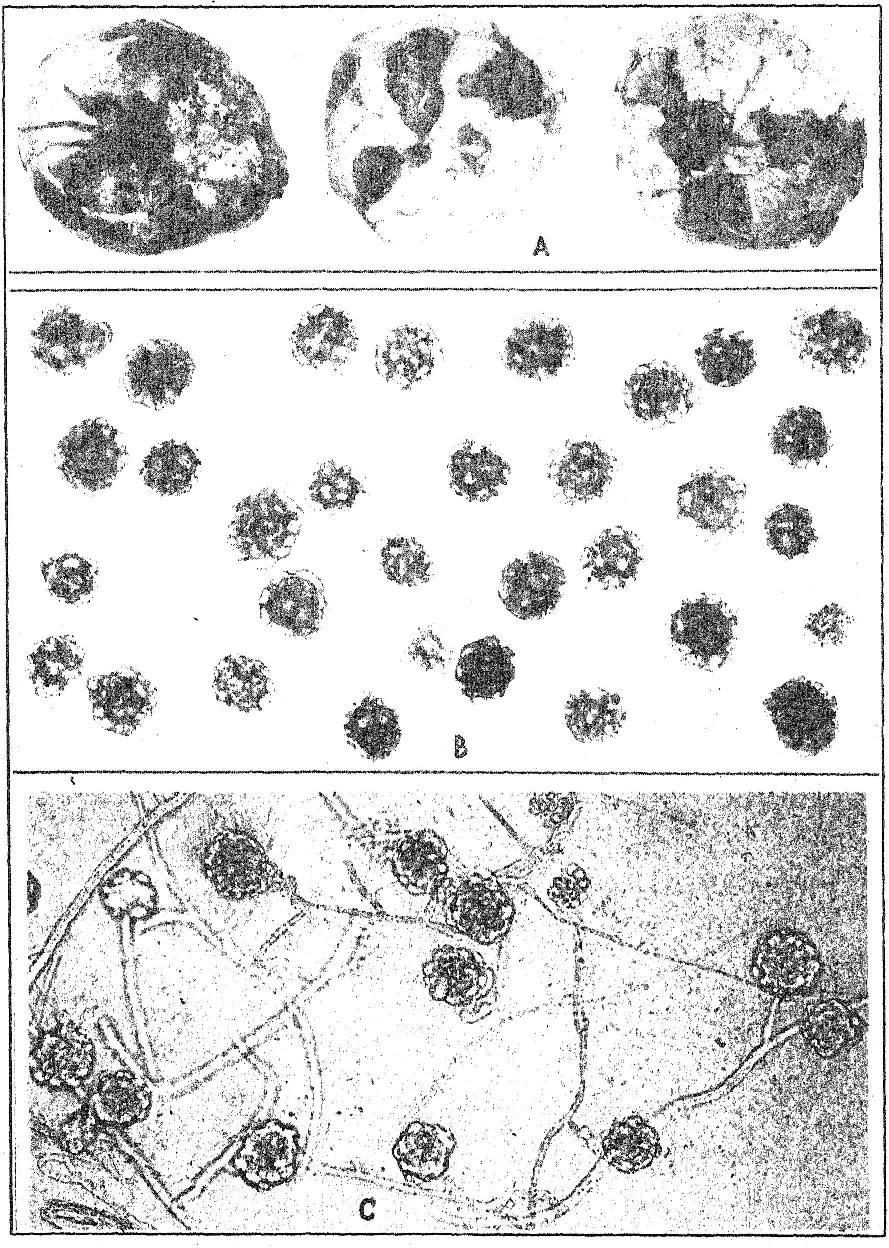

FIG. 1 A. Corms showing types of lesions and mummifications on which mats of mycelium and bulbils of *Papulaspora Gladioli* are formed; B, various types of bulbils; C, bulbils on stalks and characteristic mycelial hyphae.

even more nuclei; the hyphal cells are also multinucleate (fig. 2 E, F). The cytological picture alone would serve to distinguish the bulbils of our *Papulaspora* from the spore-balls of a *Urocystis*. The mycelium is also quite unlike that of a *Urocystis*. It is more like the mycelium of an Ascomycete, such as *Pleurage* or *Ascobolus*. The senior writer (Dodge 1920) proved by single ascospore cultures that *Ascobolus magnificus* has a *Papulaspora* stage (*P. magnifica* Hotson). The bulbils have, as a rule, a single large central cell which is multinucleate, as are the outer pale brown border cells and the cells of the vegetative hyphae. This *Ascobolus* is heterothallic so that races from single ascospores bear only bulbils. When two races of opposite sex are mated, not only bulbils but also ascocarps are developed.

On germinating, smut spores form some sort of a promycelium and the nucleus undergoes reduction. The cells of these bulbils of *Papulaspora* germi-

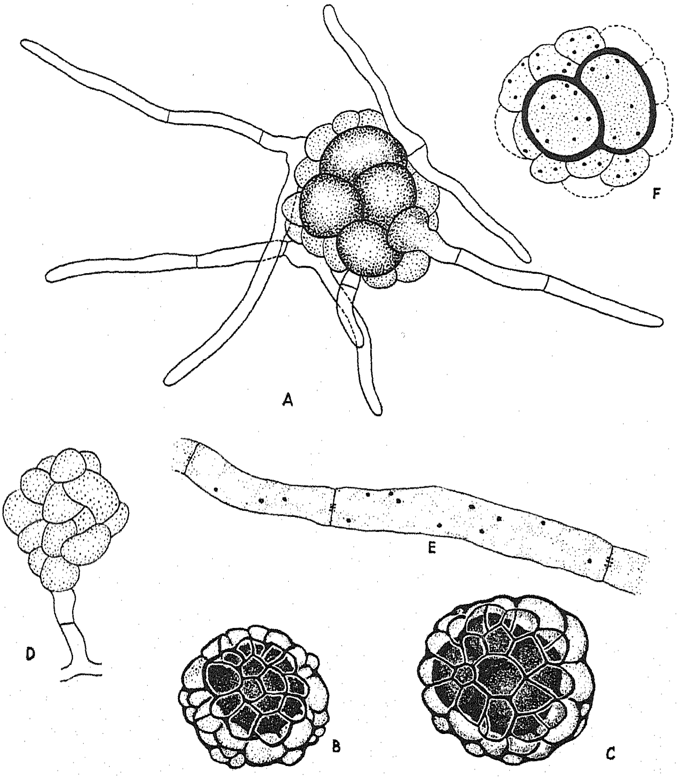

FIG. 2 A. Method of germination of bulbil. The hyaline swollen germ tube basal cell is more or less characteristic, something like the pro-germtube of ascospores of *Neurospora;* B, bulbil with one large central cell; C, bulbil with 3 central cells; D, young bulbil and its stalk; E, multinucleate hyphal cells; F, semidiagrammatic figure showing location of nuclei in a section 5 μ thick of a bulbil. (Drawings by W. L. Graham.)

nate very readily (fig. 2 A) with simple or branching germ tubes, which develop into ordinary hyphae with vacuolate cells and very definite cross-walls upon which there are several deeply staining granules (fig. 2 E). Figure 1 C shows the bulbils borne laterally on stalks.

The fungus grows very readily on manure, decaying fruit and vegetables, and various agar media. Once it becomes established in the soil of a gladiolus planting or in storage houses on debris, it could easily develop whenever conditions were suitable as they are on corms which are diseased or decaying. *Penicillium* certainly aggravates storage troubles. The *Papulaspora* may live mostly as a saprophyte, but also as a very weak parasite, furthering rot or disease primarily due to some other agent.

Smith (1876), who first illustrated spore-balls of *Urocystis Gladioli*, was a real artist. He showed cells of the bulbils readily breaking apart just as they do in spore-balls of *Urocystis*. His illustrations are very diagrammatic, so that the separation of the fertile from the sterile cells may have been idealistic. Brefeld, Magnus, and many noted mycologists have since upheld Smith's conclusions, but it should be remembered that his work on fecundation in *Coprinus* and the formation of oöspores by *Phytophthora infestans* has long since been discredited.

Since there seems to be little question that the fungus heretofore reported as *Urocystis Gladioli* Requien (Smith) is a good *Papulaspora*, we propose to call it *Papulaspora Gladioli* until some one finds the perfect stage. If Requien's type is a leaf smut the combination would simply be *Papulaspora Gladioli* (Smith). *Uredo Gladioli* Requien was described in 1830, so that the specific name will hold if one is guided by common sense and not by the style demanded by the rules of nomenclature prevailing at the moment.

The genus *Papulaspora* was established by Preuss (1851), the type species being *P. sepedonioides*. His colored plate shows the fungus on decaying apple, and mycelial wefts bearing many sporeballs on lateral branches. In general the illustrations would serve very well for *P. Gladioli*, although in detail there are some important differences (fig. 1 B, C). Hotson (1912) adopts the spelling *Papulospora*, but the original spelling by Preuss is *Papulaspora*, which he used on two different occasions the same year.

We have examined specimens of several species of *Papulaspora* in the herbarium of the New York Botanical Garden. Much of this material had been examined by Hotson in former years. Of these *P. rubida* is perhaps most similar to *P. Gladioli*. Specimens identified as *P. sepedonioides* by Sturgis have bulbils which are too small for our fungus. We are not concerned here with listing synonyms, but we wish to include in the emended description measurements of the bulbils and one or two other diagnostic features. The original description of *Uredo Gladioli* by Requien (Duby 1830) is as follows:

"U. Gladioli (Requien in herb. DC.) bifrons, maculis circà lutescentibus, acervulis nigris suborbicularibus sparsis confertisque convexis epidermide bullata clausa tectis, sporidiis subglobosis sessilibus reticulo pellucido tenuissimo obvolutis—In Gladiolo circa Avenionem (cl. Req.).''

Smith's account (1876) of the fungus on corms is more to the point: ''Sori (or clusters of spores in blisters) obliterated or effused, spores large, compound, consisting of from 3 to 6 inner cells and a larger indefinite number of transparent outer cells, both series of cells being fertile. Habitat—On and in corms and scapes of Gladioli.'' Smith saw mycelia of various fungi and as decomposition progressed the corms were totally destroyed by ''diverse fungi, infusoria, nematodes and mites.'' The ''disease'' was common in England that year, but he does not say the spore-balls were found on more than the one corm first mentioned.

Our emended description follows:

Papulaspora Gladioli (Requien) Dodge and Laskaris, comb. nov. Mycelium white at first, procumbent, profuse, matted; hyphae septate, cells multinucleate; bulbils on septate stalks, from light to dark brown in mass, spherical, 29–64 µ in diameter with from 1 to 6, occasionally more, central dark brown, multinucleate cells surrounded by a single layer of light brown cortical cells, each with several nuclei. Bulbil primordium a lateral branch ending in a coil. Cells of bulbils germinate with simple or branched germ tubes; in culture bulbils mature quickly, from 4 to 10 days; conidia not seen.

Moore (1939) of England gives the symptoms of the disease in some detail in the paragraph ''Smut, Urocystis Gladioli (Req.) (W. G. Sm.).''

''Leaden-coloured, rounded weal-like swellings with yellow margins occur on the corms, stems and leaves of affected plants. Later the skin over these swellings splits, and the dark brown powdery spore masses of the fungus lying below it are exposed. Badly attacked corms may be destroyed and reduced to a blackish-brown powder that consists almost entirely of the spore balls.''

This description is clearly a free translation of that given by Pape (1927). Moore includes along with his description a number of references from which it would seem that Van Poeteren (1924–29) at one time carried on experiments for the control of the ''smut'' disease, which had been troublesome in Holland, especially on the variety Peach Blossom. It was found that by dipping the corms before planting for a period of not more than one half hour in water kept at 110° F. (43.3° C.) the fungus can be killed and the disease controlled. We have immersed cultures of *Papulaspora Gladioli* in water maintained at 44° C. for a half hour. Transplants from the treated culture gave abundant germination of the bulbils within twelve hours. Treating the corms at 43.3° C., therefore, would certainly not be very effective.

Pape (1939) says the sori are also found on leaves and stems. We can not believe that *Papulaspora Gladioli* would be sufficiently parasitic to attack living green leaves or stems.

SUMMARY

The so-called smut disease on gladiolus heretofore considered to be caused by *Urocystis Gladioli* (Req.) Smith, has been shown to be a species of the form genus *Papulaspora*. The multinucleate condition of the hyphal cells, central and border cells of the bulbil, and the method of germination all clearly indicate that the fungus is not a smut fungus. Neither a fusion nucleus nor a promycelium at germination is evident, and mature spore-balls are formed in culture within a week's time. The bulbils are produced on side branches of a mycelium which grows more or less superficially on diseased corms. Powdery masses of the dark brown bulbils enclosed beneath the scales or in cavities in shrunken diseased tissue simulate sori of *Urocystis* chlamydospores. An emended description is given and a new combination, *Papulaspora Gladioli*, is proposed.

THE NEW YORK BOTANICAL GARDEN
NEW YORK, NEW YORK

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VALIDITY OF EQUATIONS FOR RELATIVE GROWTH CONSTANTS WHEN APPLIED TO SIGMOID GROWTH CURVES[1]

ROBERTSON PRATT

(WITH SEVEN FIGURES)

Huxley (1924, 1932) showed that in many different kinds of organisms the relative magnitudes of parts growing at different absolute rates may be expressed approximately by the equation

$$y = bx^k \tag{1}$$

which may be written

$$\log y = \log b + k \log x \tag{2}$$

where y represents the magnitude of one differentially growing part, x represents the magnitude of the rest of the plant or animal body, or of another part to be compared with the first, b is a constant that indicates the value of y when $x = 1$, and k is a constant that denotes the ratio of the relative growth-rate of the part to the relative growth-rate of the rest of the body, or of the other part.[2] Values of x and y that satisfy this equation locate a straight line when plotted on logarithmic scales.

However, although the formula is a convenient tool and its application to biological data often reveals interesting relations among differentially growing quantities, its use is restricted by definite limitations. This fact was appreciated by Huxley (1932) but seems to have been overlooked by several later investigators who have applied the equation indiscriminately to their experimentally obtained data. The use of this formula has been critically discussed in an earlier theoretical paper (Lumer, 1937).

The purpose of the present report is to emphasize the proposition that double logarithmic plotting of growth data is not a satisfactory substitute for the original data plotted as time curves and that when it is found for any particular set of data that logarithmic plotting according to equation 2 yields approximately a straight line of a certain slope, the parts of the growth cycles for which this applies should be accurately defined because for other parts the slope will be different unless the entire growth cycles coincide.

Huxley (1932) pointed out that the validity of equation 1, as far as its application to growth data is concerned, rests on the assumption that ". . . since the organ and the body have both existed for the same length of time when we measure them, the time factor cancels out. . . ." It seems of interest to examine this statement with respect to sigmoid curves, since it is this type of curve that is most frequently encountered in studies of the growth of multicellular organisms. It will be shown that even when the organs under consideration "have both existed for the same length of time" when they are measured, the time factor may not always be justifiably cancelled out unless the entire growth cycles are of equal duration.

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[1] The ideas presented in this paper are in some measure the outcome of discussions with Professor Sam F. Trelease at Columbia University during the years 1935–1937 and of subsequent discussions with him. His interest in the manuscript is keenly appreciated. The author accepts full responsibility, however, for the validity of the statements made and for the manner of their expression.

[2] Huxley (1932) defined relative growth-rate as the rate of growth per unit weight. Of course it might also be per unit height, volume, or any other measurable quantity.

The curves in figures 1 to 7 show empirically that for organs with sigmoid growth curves, the statement quoted above may be approximately true for portions of the growth cycle; but it should be emphasized that the equation is a precise representation of the facts for the complete period of growth only when the entire growth periods of the quantities under consideration are of equal duration and coincide in absolute time. For a complete picture of the relative growth of two organs (or numbers) the actual measurements and the times at which they were made should be included as the basic experimental data, so that the reader may know just what part of each growth cycle is under consideration, and how the lengths of the entire growth periods compare.

The mathematical analysis and interpretation of sigmoid growth curves is not yet entirely satisfactory, but numerous investigators have shown that the rate of growth of many multicellular organisms and of their parts may be represented approximately by the equation

$$\frac{dx}{dt} = k\,x\,(A - x) \tag{3}$$

Upon integration this becomes

$$\log \frac{x}{A - x} = K\,(t - t_1) \tag{4}$$

which is the equation for the symmetrical sigmoid curve that is characteristic of auto-catalyzed monomolecular reactions. This equation does not always furnish a precise representation of the normal growth curve, but is the simplest expression that affords a reasonably accurate approximation of the sigmoid curves obtained experimentally (Robertson 1908a, 1908b, 1923; Gaines and Nevens 1925; Reed 1920, 1928, 1932; Reed and Holland 1919; Porterfield 1928; Pratt 1936, 1937, 1940; Pratt and Fong 1940; Sideris and Krauss 1938; Albaum, Kaiser, and Eichel 1940). $K = kA/2.3$; x represents the magnitude of the organ or organism at time, t; A denotes the final value of x, and t_1 is the time when $x = A/2$. K is a constant that represents the slope of the straight line that results when values of $\log\,[x/(A-x)]$ are plotted as ordinates against values of $(t - t_1)$ as abscissas. It is apparent that K is an inverse function of the time required for the growth cycle to reach completion. Several ideal curves of the form described by equation 4 are drawn in figures 1 and 2.

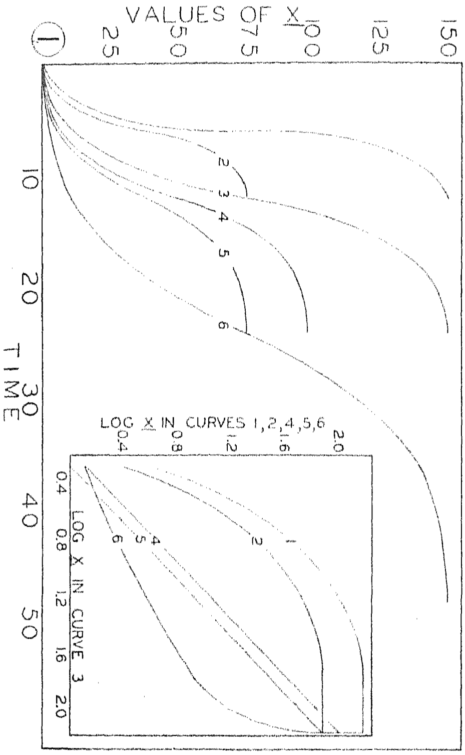
When the growth periods are equal and coincide in time (curves 3, 4, and 5, figure 1), double logarithmic plotting after the manner of Huxley (inset, figure 1) yields a straight line with slope = 1.0. It is clear that the slope can have no other value, since if x and x_1 represent the magnitudes of two quantities, and A and A_1 denote the final values of x and x_1, respectively, then from equation 4 (values of K and t_1 being the same for one curve as for the other) at any time, t

$$\log \frac{x_1}{A_1 - x_1} = \log \frac{x}{A - x} \tag{5}$$

and, therefore, $x_1 \propto x$. Under these conditions, equation 1 becomes simply $y = b\,x$; as the two parts grow, one is always a simple constant multiple of the other.

When the total growth periods are unequal (curves 1, 2, and 6 compared with curve 3 in figure 1) or when they are equal in length but do not coincide in time as, for example, when one organ begins to grow later or ceases growing sooner than another (figure 2), a straight line cannot accurately fit all of the points. The divergence of the curve from a straight line with slope = 1.0 increases as the inequality in length of the growth periods or difference of time increases. The slope of the logarithmic curve approaches, and finally attains, a value of zero as the curve becomes horizontal, or increases without limit as the curve approaches a vertical position. It should be pointed out, however, that even when there is considerable difference in the growth periods, double logarithmic plotting following equation 2 of data from isolated portions of the growth cycles may yield curves that are approximately linear over relatively wide ranges (insets, figures 1 and 2), although the slopes have very different values for the first and last parts of the growth cycles. It is evident, therefore, that when logarithmic plotting gives approximately a straight line of a certain slope, the parts of the growth cycles for which this is true must be defined accurately, since the slope will be different for other parts unless the total growth periods coincide.

Frequently when growth data are plotted according to equation 2, they seem to be fitted best by two straight lines with more or less widely differing slopes, and several investigators have attempted to ascribe biological significance to the break that occurs in these curves. When the original data are not given as time curves or in tables, it is difficult for the reader to evaluate such conclusions. It should be pointed out, however, that several of the curves in the insets of figures 1 and 2 might, if based on biological data which generally show greater or less variation, be easily thought to represent two straight lines with different slopes. It is apparent, therefore, that such a curve does not necessarily indicate any pronounced change in the metabolism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50
75
100
125
150
TIME
10
20
30
40
50
2
3
4
5
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LOG X IN CURVES 1,2,4,5,6
0.4
0.8
1.2
1.6
2.0
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0.8
1.2
1.6
2.0
1
2
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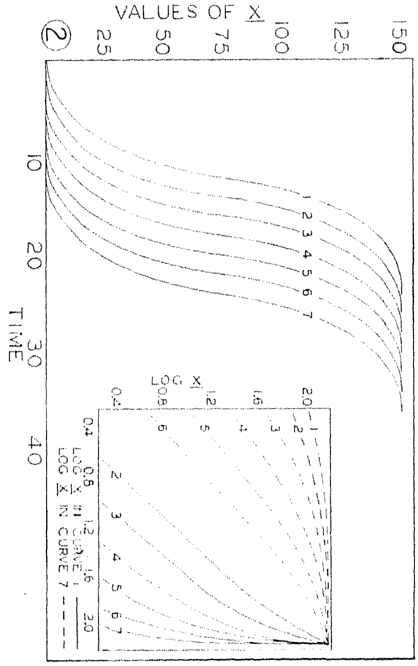
6

①


VALUES OF X
25
50
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TIME
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4
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LOG X
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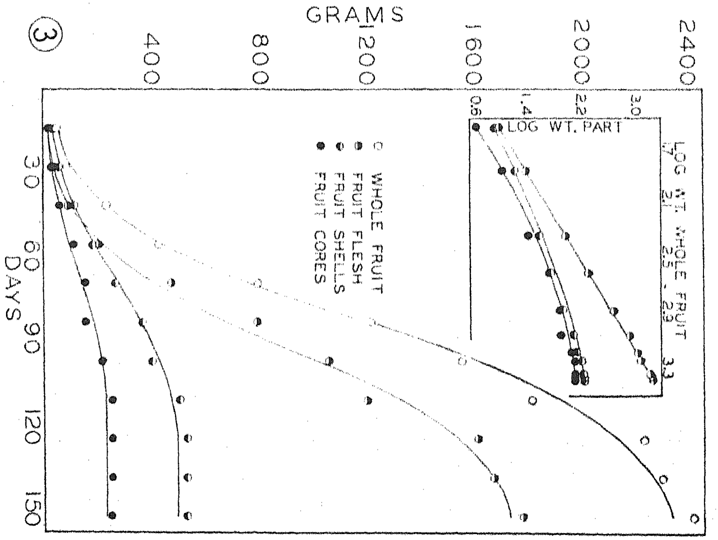
LOG X IN CURVE 1 ——
LOG X IN CURVE 7 - - -

②


GRAMS
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800
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1600
2000
2400
DAYS
30
60
90
120
150
○ WHOLE FRUIT
◐ FRUIT FLESH
◑ FRUIT SHELLS
● FRUIT CORES
LOG WT. PART
0.6
1.4
2.2
3.0
LOG WT. WHOLE FRUIT
1.7
2.1
2.5
2.9
3.3

③

or physiological activity of the organs but may be merely the inevitable result of comparing two quantities whose periods of increment are not entirely concurrent.

The relations discussed above are not peculiarities of "ideal" sigmoid curves. This is shown by figures 3–7 and table 1 where experimentally obtained data are presented. The integrated growth curves are all of the sigmoid type, those of Porterfield, of Pratt, and of Sideris and Krauss being reasonably accurately described by an equation with the general form of equation 4 or a simple modification of it.

It should be noted that in all cases where the growth periods do not coincide the slopes of the logarithmic curves vary from finite values to infinity or zero, although the logarithmic plots seem to be approximately linear for certain discrete portions of the curves considered separately. The departure from a straight line increases with the disparity of the total growth periods; but when different quantities increase in a sigmoid manner through approximately the same period of time, double logarithmic plotting yields

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FIG. 1. Curves drawn according to the equation $\log \frac{x}{A-x} = K(t-t_1)$ where x (ordinate) represents the magnitude of the quantity under consideration at any time, t; A denotes the final value of x, and t_1 is the time when $x = A/2$. K is a constant that varies inversely with the time required for the growth cycle to reach completion. The different curves have the following constants:

	A	K	$2t_1$ = full length of growth period
Curve 1	150	0.374	12
" 2	75	0.374	12
" 3	150	0.187	24
" 4	98	0.187	24
" 5	75	0.187	24
" 6	150	0.094	48

Inset: Logarithms of values of x in curves 1, 2, 4, 5, and 6 plotted as ordinates against logarithms of values of x in curve 3 at corresponding times. FIG. 2. Curves drawn according to the equation $\log \frac{x}{A-x} = K(t-t_1)$. In each curve, $A = 150$, $K = 0.187$, and the total growth period = 24. Each curve is separated from the next one by two units on the abscissa, so that although all the curves increase for the same length of time the growth periods do not coincide. *Inset:* Solid lines show logarithms of x from curves 2, 3, 4, 5, 6, and 7 (ordinates) as functions of log x in curve 1 at corresponding times. Discontinuous lines show log x from curve 7 on the abscissa scale and log x from the other curves on the ordinate. FIG. 3. Growth of whole fruits and of their parts in the pineapple (*Ananas sativus*). *Inset:* Logarithmic plotting to show the relative growth of the parts compared with the whole fruit. The integrated curves are drawn according to the equation $\log \frac{x+a}{A-x} = \log \frac{a}{A} + Kt$ where x, A, K, and t have the same significance as in equation 4 and where a represents the value of x when $t = 0$. The points indicate experimental observations. The data were taken from Sideris and Krauss (1938).

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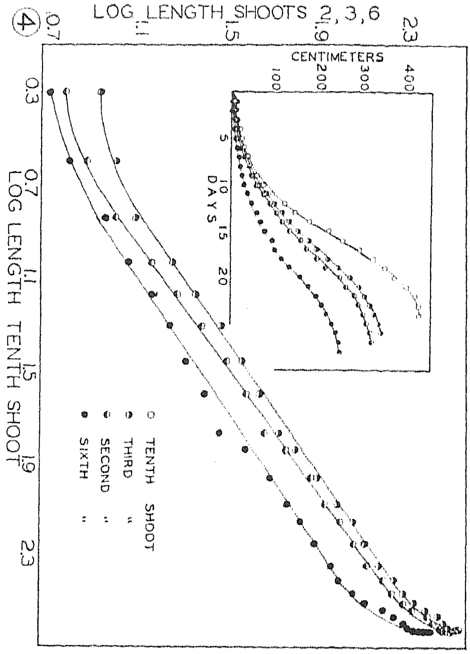
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1.1
1.5
1.9
2.3
LOG LENGTH TENTH SHOOT
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0.7
1.1
1.5
1.9
2.3
CENTIMETERS
100
200
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○ TENTH SHOOT
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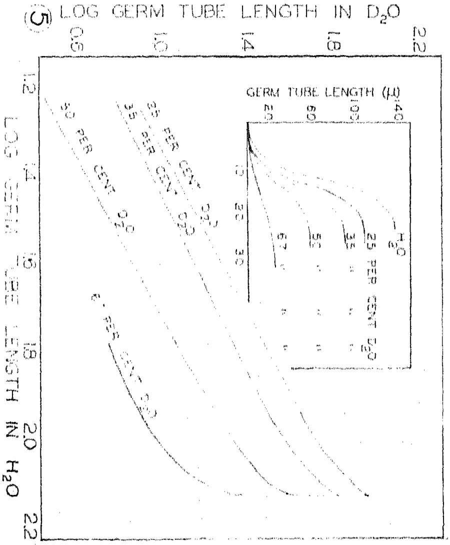
● SIXTH "

⑤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1.0
1.4
1.8
2.2
LOG GERM TUBE LENGTH IN H_2O
1.2
1.4
1.6
1.8
2.0
2.2
GERM TUBE LENGTH (μ)
20
60
100
140
10
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H_2O
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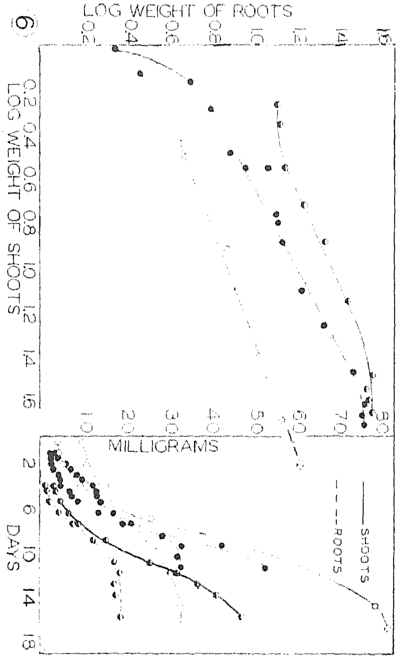
67 PER CENT D_2O

⑥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0.4
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1.0
1.2
1.4
1.6
LOG WEIGHT OF SHOOTS
0.2
0.4
0.6
0.8
1.0
1.2
1.4
1.6
MILLIGRAMS
10
20
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DAYS
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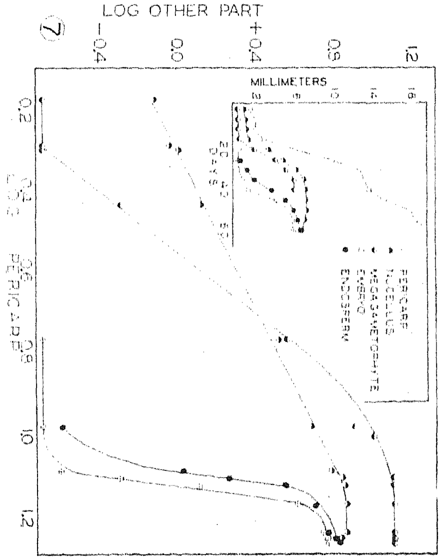
—— SHOOTS
- - - ROOTS

⑦


LOG OTHER PART
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0.0
+0.4
0.9
1.2
LOG PERICARP
0.2
0.4
0.6
0.8
1.0
1.2
MILLIMETERS
DAYS
20
40
60
PERICARP
NUCELLUS
MEGAGAMETOPHYTE
EMBRYO
ENDOSPERM

straight lines for the entire growth periods and k values are approximately 1.0 (table 1). Thus it may be seen that the empirical observations are in agreement with expectations based on theory.

It is of interest now to examine some of the data on "chemical heterogony." Numerous investigators have studied the chemical composition of animals at different stages of development and some have employed the Huxley formula to describe the relative abundance of chemical constituents in the organisms, or their parts, at different times. Needham (1934) summarized and reviewed many sets of these data. Seventeen substances and twenty-six species of animals ranging from Crustacea to mammals were considered, and it was found that in nearly every case a straight line resulted when the logarithm of the magnitude of the chemical entity at any time was plotted against that of the chemical totality, i.e., dry or wet weight, at the same time.

A portion of Needham's paper is devoted to speculation concerning the "general significance" of the fact that "... organisms of extremely different morphological form give identical differential growth ratios for a given chemical substance" and it was suggested that "genetic differences and interphyletic differences occur only at a supra-chemical level."

It should be observed, however, that not only were the differential growth ratios "identical" for a given chemical substance, but that they were essentially the same for most of the substances studied, i.e., about 1.0. Most of the

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FIG. 4. Logarithmic plots to show the relative growth rates of different shoots of bamboo, *Phyllostachys nigra*. *Inset:* Original data plotted arithmetically. The data were taken from Porterfield (1928). FIG. 5. Logarithms of *Erysiphe* germ tube lengths in different concentrations of heavy water (ordinates) as functions of logarithms of germ tube lengths in ordinary water at corresponding times. *Inset:* Original data plotted arithmetically. The curves are drawn according to the equation $\log \frac{x}{A-x} = K(t - t_1)$ and have the following constants:

	A	K	$2t_1$ = full length of growth period
H_2O	136.8	0.187	24.76
25 per cent D_2O	110.7	0.183	27.50
35 " " "	91.0	0.165	27.26
50 " " "	59.4	0.174	28.00
67 " " "	24.5	0.127	32.50

The data were taken from Pratt (1936) and from unpublished material.

FIG. 6. *Left:* Logarithmic plots to show the relative growth-rates of roots and shoots in different lots of peas (*Pisum sativum*). *Right:* Arithmetic plots of original data. The data were taken from Pearsall (1923). FIG. 7. Logarithmic plots to show the relative growth rates of different parts of the fruit in an early-ripening variety (Early Purple Guigne) of sweet cherry, *Prunus avium*. Curves labelled nucellus and megagametophyte, respectively are for nucellus + integuments and for megagametophyte + embryo sac. *Inset:* Original data plotted arithmetically. The data were taken from Tukey (1933).

sets of data analyzed by Needham pertain only to the early stages of growth when the rates of increase were rising, but it seems reasonable to assume that had data for the entire life of each of the different organisms been plotted, sigmoid curves would have resulted. It may also be reasonable to assume that in a given organism, permitted to grow to maturity, the different substances (“chemical entities”) studied would have increased through approximately the same period of time as the dry or wet weight (“chemical totality”), i.e., as long as the organism continued to grow. Hence, heterogonic plots based on theoretically ideal data for each organism would have yielded straight lines with slope = 1.0. The mean value of k calculated from sixty-nine published observations (Needham 1934) is 1.1 ± 0.02. This is remarkably close to the expected value of 1.0, when allowance is made for the normal variation of living organisms, the diverse conditions under which the data were obtained, and the fact that the value of k in each case depends largely upon the statistical accuracy of each of the individual sets of data on which it is based. It seems, therefore, from the discussion presented above that perhaps one should not be too prone to attach special significance to the “uniformity of chemical heterogony in widely different organisms.”

As similar examples from the botanical literature, the studies of Gaines and Nevens (1925) and of Bisson and Jones (1932) on the chemical composition of sunflower and pea crops respectively have been selected. The data have been plotted after the manner of Huxley and the k values calculated. The average values of k for the total carbohydrate and total nitrogen (substances for which the data seem most reliable) are 0.99 and 0.96 respectively. These values of k and those for the different mineral components which also increased during approximately the same period of time as the dry weight

TABLE 1

Components of pea and sunflower plants as functions of dry weight[1]

Component of plant	Plant	Investigator	k = relative growth constant
Total carbohydrate	Pea seeds	Bisson and Jones	0.98
“ “	Sunflower seeds	Gaines and Nevens	0.97
“ “	“ crops	“ “ “	1.02
“ ash	Pea seeds	Bisson and Jones	0.95
“ “	Sunflower seeds	Gaines and Nevens	0.83
“ “	“ crops	“ “ “	0.84
“ nitrogen	Pea seeds	Bisson and Jones	0.92
“ “	Sunflower seeds	Gaines and Nevens	0.99
“ potassium	Sunflower seeds	“ “ “	0.94
“ sulphur	“ “	“ “ “	0.99
“ magnesium	“ “	“ “ “	1.02
“ calcium	“ “	“ “ “	0.72
“ phosphorus	“ “	“ “ “	0.84
		Av. value of k =	0.92

[1] The periods of increment of the different components listed and of the dry weight, with which they were compared, were nearly coincident in all of the plants listed.

are shown in table 1. The mean value of k is 0.92, a figure remarkably close to the expected value of 1.0.

It should be emphasized that the remarks made in this paper pertain specifically to sigmoid growth curves. Many other kinds of growth curves will give straight lines when plotted according to Huxley's formula. When this is so, it means merely that the slope of one original semi-logarithmic curve (log size against time) is always a constant multiple of the slope of the other. The constant factor by which the two slopes differ represents the slope, or k value, of the Huxley line. If the original semi-logarithmic curves have the same slopes during the same time intervals, the Huxley k is 1.0.

SUMMARY

Application of the Huxley equation $y = bx^k$ to growth data in order to express the relative growth-rates of different organs often reveals interesting relations among differentially growing quantities. Its use is restricted by definite limitations, however.

When the equation is found to fit the observed data, the parts of the growth cycles to which it applies should be accurately defined, because for other parts the slope of the logarithmic curve (k value or "relative-growth constant") may be quite different.

Logarithmic plotting of growth data in accordance with the Huxley formula is not a satisfactory substitute for the original data plotted as time curves.

If the growth cycles of the two quantities coincide in time and follow the sigmoid course of the curve for an autocatalytic monomolecular reaction that is characteristic of the growth of many multicellular organs and organisms, the k value, or relative growth constant, as determined by the Huxley equation, is 1.0. The value of y then remains a simple multiple of x; i.e., $y = bx$.

When the total growth periods are unequal or when they are equal but do not coincide in time, a straight line cannot accurately fit all of the points, although isolated portions of the growth cycles may yield curves that are approximately linear over relatively wide ranges. The slopes may have very different values for the first and last parts of the growth cycles, however, approaching a value of zero as the curve becomes horizontal, or increasing without limit as the curve approaches a vertical position.

A sharp break in the relative-growth curves does not necessarily indicate a fundamental physiological change in the organism as some investigators have suggested, but may be merely the inevitable consequence of comparing two quantities whose periods of increment are not entirely concurrent.

The remarks in the present paper refer specifically to relative-growth constants of quantities that increase as sigmoid functions of time. They are not intended to apply to other types of growth curves, although it is possible they could be extended to cover other cases also.

The statements and conclusions of the present paper are supported empirically by "ideal" curves calculated from equations commonly employed in growth studies and by curves constructed from data in the literature.

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San Francisco, California

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THE INFLORESCENCE IN HEMEROCALLIS—I

A. B. STOUT

(WITH TWENTY-TWO FIGURES)[1]

THE ORIGIN OF THE SCAPE

In *Hemerocallis* the plant is an herbaceous perennial and the numerous, short, somewhat thickened, and much intertwined branches in the crown of the plant bear coarse, grass-like, and closely equitant leaves in two ranks which rise from a crown-branch into the air as "fans." A flower scape arises from a leafy stem in the crown and is terminal for the axis immediately below it.

When a scape is located in the center and apex of a fan of leaves its terminal position is evident. It stands between the concave and upper surfaces of the two leaves which arise from the two nodes which are immediately below the scape and of the same axis; and vegetative laterals are lacking in the axils of either of these leaves. The relation of the axis and the two leaves is as shown in figure 1 for the leaves labeled *L2* and *L3*.

Frequently a scape appears to be a lateral on the stem of a single fan of leaves. But in such cases the vegetative shoot that appears to rise above the base of the scape is the real lateral that arises in the axil of one of the uppermost leaves of the main axis that continues into the scape. Figure 1 shows the relationships when the vegetative shoot is in the axil of the uppermost leaf (fig. 1, *L3*) that clasps the base of the first internode of the scape. When but one vegetative lateral develops and is located in the axil of the next to the last leaf, the scape also stands between two equitant leaves but now the leaf that clasps the base of the scape has no axillary branch.

A scape may stand between two vegetative branches ~~(see fig.~~ 2), in which case the main axis that continues into the scape has two laterals; one may arise in the axil of the leaf that clasps the base of the first internode (*L3* of fig. 2) of the scape and one is in the axil of the next leaf below (*L2* of fig. 2). These two branches are on opposite sides of the scape which now stands between the convex surfaces of two leaves (*L3–1* and *L4–1* of fig. 2) each of which belongs to a different lateral. During a single period of flowering two scapes may arise as successive terminals in a single fan of leaves.

In the formation of a scape, its first segment or internode is greatly modified, especially in respect to elongation and to reduction in diameter, in contrast to the internodes immediately below it and to those of any lateral in the crown (compare internode *4* with *3* and *4–1* in fig. 1). When a scape appears to be a lateral it is the vigorous vegetative growth of its own basal lateral as a leafy crown-branch that continues the two ranks of leaves in such a manner that the shift from terminal to a lateral is not obvious to casual observation. But the arrangement of the leaves about the base of the scapes clearly indicates that a scape is terminal on the axis immediately below it.

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[1] Assistance in the preparation of the figures of this article was furnished by the personnel of the Works Progress Administration (O.P. 165-1-97-8. W. P. 5).

THE SIMPLE INFLORESCENCE OF H. NANA

In the species *Hemerocallis nana* the flowers are solitary and terminal for the main axis of the scape and for each of the few laterals which develop on the scape. There are no traces in the axils of the bracteoles of the laterals which, in all other species now recognized, form the bostryxes of the inflorescence.

The one-flowered scapes. Frequently the normally developed scapes on plants of *H. nana* bear a solitary flower below which there are two modified leaves (fig. 3). These are placed not far below the flower and the upper and smaller one (a bracteole) is often clearly placed on the axis at an angle that is approximately 90° from the position of the lower one (a bract).

The distribution of vascular bundles in a typical single-flowered scape

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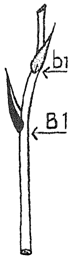
Explanation of figures 1–16

All figures except 1, 2, 9, and 10 are approximately one-half natural size. In most cases the drawings were made for scapes that had ended flowering. Most capsules and flowers, if present, were omitted and the ends of pedicels shown as when the flowers absciss below the ovary. In the lettering the designations are as follows: *L*, leaves of crown branches; *B*, bracts on the main axis of a scape; *SB*, bracts on lateral branch; *VD*, vegetative dichotomy of which both arms continue as an internode until there is a bract; *b*, bracteole, also not so heavily shaded as bracts; *f*, flower; Roman numerals (I, II, III) indicate succession in development and blooming.

FIG. 1. Lower portion is diagram of section showing relations and positions of parts when a scape has a vegetative crown lateral that is axillary to the leaf (*L3*) that is located at the base of the first internode of the scape. Upper portion shows a scape of *Hemerocallis minor* with a primary inflorescence of two bostryxes, below which there is a lateral branch bearing only one flower. FIG. 2. Diagram of sectional view of a scape which has a vegetative crown lateral in the axil of each of the two uppermost leaves (*L2* and *L3*) of its crown axis. FIGS. 3–8 inclusive. Scapes of *Hemerocallis nana*. FIG. 9. Nondichotomous bostryx of *Alstroemeria revoluta*. Copied from illustration by A. and L. Bravais. FIG. 10. Dichotomous bostryx of *Hemerocallis fulva* clone Europa. Copied from illustration by A. and L. Bravais. FIG. 11. A two-bostryx primary inflorescence of the Europa daylily at the time when the first flower is ready to open. FIG. 12. A two-bostryx primary inflorescence of the Europa daylily after all flowers have bloomed and fallen. FIG. 13. A three-bostryx primary inflorescence of the Europa daylily. FIGS. 14, 15. Upper portion of scapes of *H. minor* showing vegetative dichotomy in the first internode of a scape. In figure 14 each bostryx is reduced to one flower; in figure 15 each is reduced to two flowers. FIG. 16. Scape of *H. minor* bearing one flower which is terminal on the lateral belonging in the axil of bract 2. The dichotomous lateral to the pedicel of this flower, the lateral in the bract below, and the terminal of the main axis above bract 3 are all aborted.



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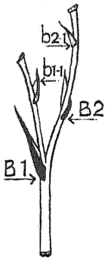

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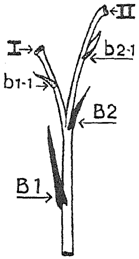

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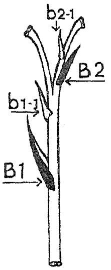

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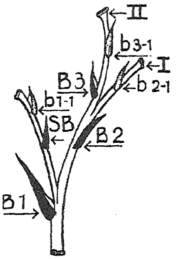

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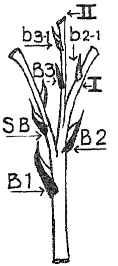

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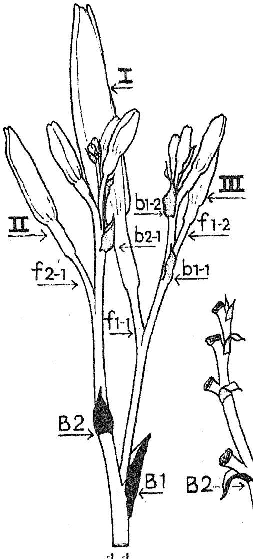

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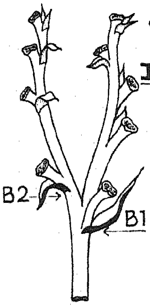

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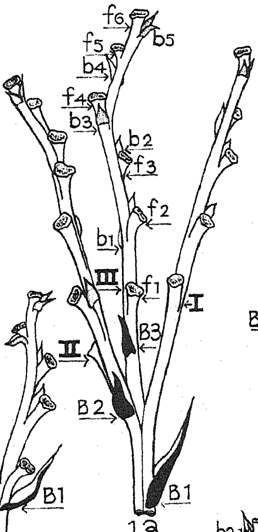

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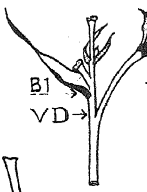

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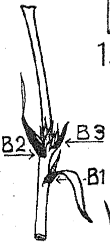

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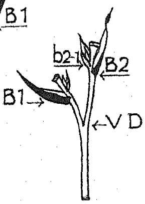

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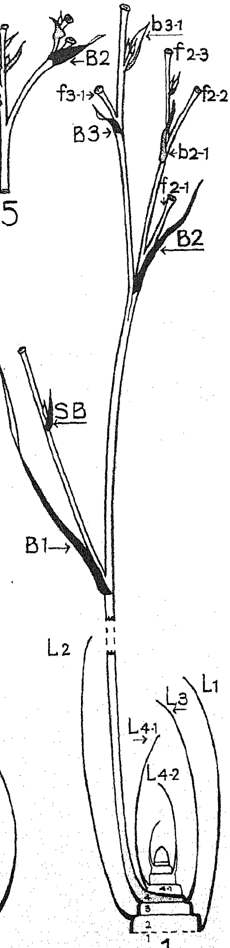

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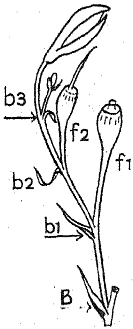

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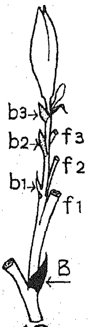

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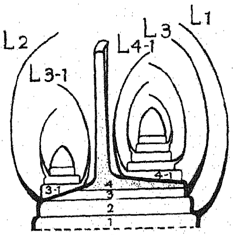

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was studied in cross-sections at levels below the bract and the bracteole, midway between the two, and above the bracteole. In the upper portion of the first internode of the scape, in a cross-section, there was a central core of pith cells about which there was a zone of cells that had thick walls (stereome tissue). Rather evenly distributed throughout the stereome there were numerous (about 35) fibrovascular bundles. In the segment of the stereome directly below the bract (as *B1* of fig. 3) the vascular bundles branched and supplied veins to the bract but no bud was organized in its axil and the main axis continued as a single stem. Immediately below the bracteole (as *b1* of fig. 3) branches of bundles in the stereome supplied veins for the bracteole but no lateral was organized and no abortion of one was present. At this level and above in the pedicel the stereome was less defined and the bundles were more equally distributed within the scape.

It seems certain that in this species the main axis of a single-flowered scape continues as a single stem throughout its first internode, through the segment between the bract and the bracteole and on into the pedicel of the flower. But the character of this axis does change: the first internode is relatively long, as much as twelve or more inches in this dwarf species, while the second internode, or peduncle, is very much shorter; the phyllotaxy changes from the two-ranked and 180° spacing to one of only 90°; in the internal structure there are a decrease of the stereome and a more central distribution of vascular bundles, especially in a pedicel.

In *H. nana* the flower of a normal single-flowered scape is obviously terminal. For the purposes of this discussion it will be considered that such a scape is differentiated into (1) a long internode which terminates at the primary bract (*B1* in fig. 3), (2) a peduncle of one internode which terminates at the bracteole (*b1* in fig. 3), and (3) a pedicel that terminates in a flower.

Two-flowered scapes (figs. 4, 5, and 6) are frequent among plants of *H. nana* and they may occur on the same plant with scapes that bear solitary flowers. In these the lower flower is the first to open, and it (fig. 4) is the terminal of a lateral that arises in the axil of the lower of two primary bracts on the main stem. In such a lateral there is an internode (which is the peduncle) and a bracteole (*b1–1* in fig. 4) above which the axis continues as a pedicel of a flower. Thus the main axis of a two-flowered scape has two internodes. The lower flower is terminal on a lateral branch and the upper flower is terminal on the main axis.

The lateral branch dominates the main axis above it in vigor of growth and in time of maturity. Often its organization as a separate axis is delayed and it is more or less combined with the main axis until the level of the second bract is reached (fig. 5). The bracteole that belongs on the lateral may even be placed (fig. 6) below the level of the complete separation of the lateral.

Three-flowered scapes. Drawings of typical three-flowered scapes from plants of *H. nana* are shown in figures 7 and 8. The two apical flowers are like those of the two-flowered scapes. Below these the main axis has an additional internode and a primary bract in the axil of which there is a lateral. In such scapes the lower of the two laterals often has an internode, a secondary bract, a peduncle, a bracteole, and a pedicel that ends in a solitary flower (figs. 7 and 8). Frequently there is delayed separation of the lower lateral (fig. 8).

All the three-flowered scapes seen by the writer were on plants that were growing in the Royal Botanic Garden at Edinburgh, Scotland, and which were at the time through blooming. When the lower lateral of a three-flowered scape of *H. nana* has a vegetative internode and a secondary bract, it seems that its flower opens later than does the flower on the lateral which is above it (figs. 7 and 8).

Irregularities in the development of scapes in plants considered to be *H. nana* have been noted. Scapes with solitary flowers have been observed which had as many as four bracts in the axils of which there were no signs of any lateral. In others there were scapes in which the main axis above the second bract was more or less undeveloped and in some cases reduced to a mere stub. The irregular and delayed separation of laterals may be such that there is the interpolation of two or more axes at one level with the placing of bracts and bracteoles at irregular positions. These features of growth are more conspicuously developed in other species of the genus in which the entire inflorescence is much compacted.

A comparison of scapes of *H. nana* which bear one flower, two flowers, and three flowers shows that the uppermost flower is terminal on the main axis and is alike in all three. The two-flowered scape has in its main axis one additional internode with a lateral to its bract. The three-flowered scape has still another internode with a bract and a lateral. Thus the additional flowers are produced by an increase in the number of internodes in the main axis and the formation of laterals.

In the species *H. nana*, as far as the writer observed, there are no indications of secondary laterals, either rudimentary or otherwise, which arise in the axil of any bracteole. In the three-flowered scape both the terminal and the lateral immediately below it have each only a peduncle and a pedicel and the two combine to form what may be called a terminal inflorescence. When a lateral below these two has an extra internode and bract and is later in the maturity of its first flower it may be considered as a secondary inflorescence.

Not only does the species *H. nana* have the simplest inflorescence of any of the known and recognized species of *Hemerocallis*[2] but it is the smallest in stature and it has, according to present knowledge, a very restricted distribution in the interior of China.

THE NATURE OF THE BOSTRYX

It now appears that, except for *H. nana*, the "dichotomous" bostryx is present in all species of *Hemerocallis*. Also two or more bostryxes combine to form a primary inflorescence that is terminal for the entire scape. In much-branched species the laterals below such an inflorescence have one or more secondary bracts above which the bostryxes form secondary inflorescences.

The nature and character of the dichotomous bostryx in *Hemerocallis* will be more readily understood if there is first a consideration of the unforked bostryx in other genera.

The nondichotomous bostryx was recognized and described as a "Schraubel" and as a "Bostryx" as early as 1835 (Schimper according to Braun 1835). Soon thereafter (1837), L. and A. Bravais designated this type of branch a "cime uninodale helicoide" and these authors made a somewhat comprehensive survey of its occurrence and modifications in the inflorescences of flowering plants. They noted that the helicoid cyme in flowering plants may be elongated or shortened, axillary or terminal, *single or dichotomous*, and that bracteoles may fail to develop, or they may be present in normal position at the base of a pedicel, or they may be transposed to other positions.

The simple (nondichotomous) bostryx or uninodal helicoid cyme was illustrated by L. and A. Bravais in the species *Alstroemeria revoluta* and their figure is here reproduced (fig. 9). In this, the first flower in a series of flowers is terminal on the axis immediately below it. In this axis there is a peduncle with one node ("uninodale") at which there is a bracteole; above the bracteole there is one pedicel which ends in a flower. But a lateral to this pedicel develops in the axil of its bracteole and continues to form a new peduncle which terminates above its own bracteole in a pedicel and its single flower. The relation of flower pedicel to its lateral is continued to form the successive flowers above until there is an abortion of the new lateral. The successive peduncles combine to form a false axis. There is but one row each of bracteoles, of units of the false axis, and of pedicels and flowers, and these are arranged in an ascending spiral which continues in one direction. It is this single, ascending, spiral arrangement with the decreasing size of the flowers, bracts, and stem units that suggested the terms "helicoid" (like a snail shell), "schraubel" (a screw), and "bostryx" (a curl). In contrast to this a double series with also a spiral arrangement was called a "scorpioid cyme" or "cincinnus."

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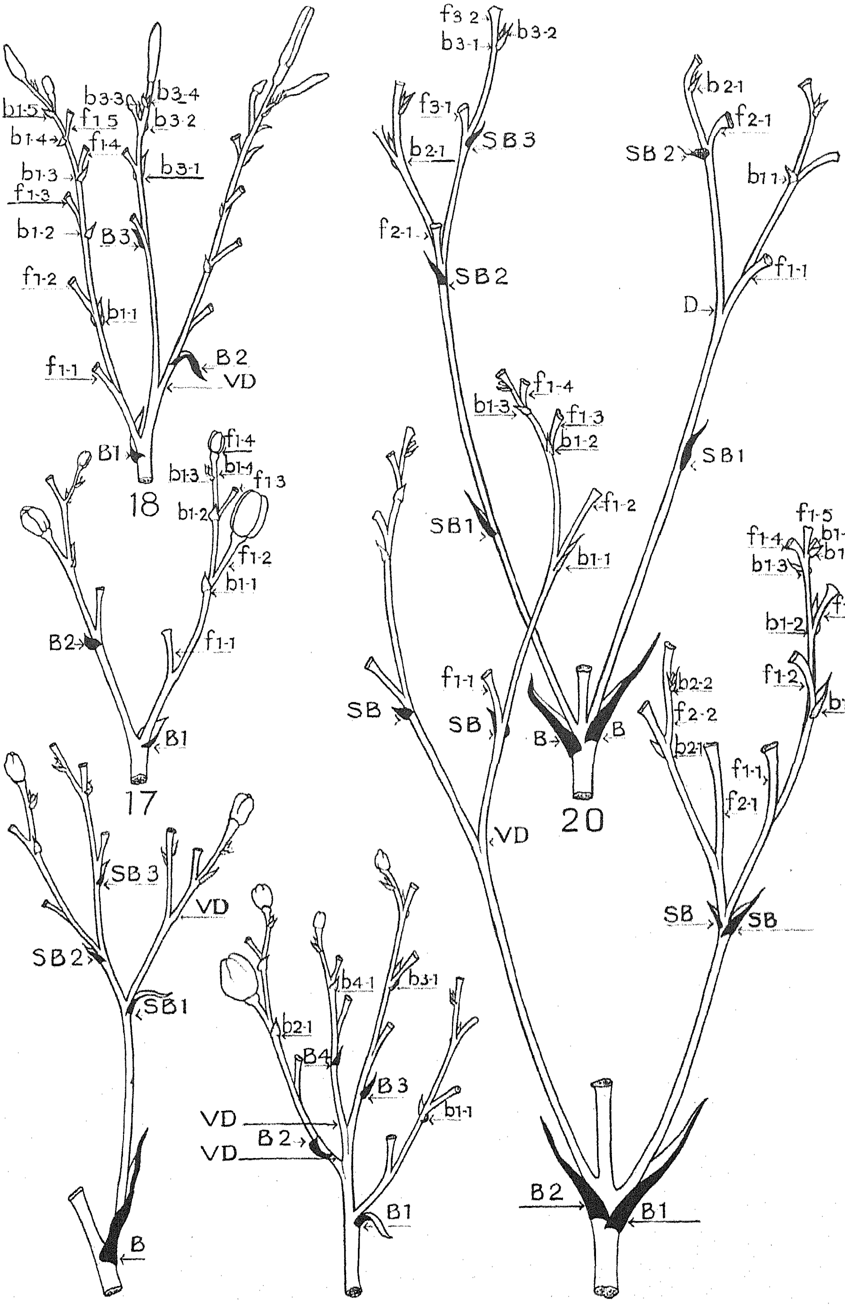
[2] At present the writer does not consider that the description and herbarium material of the so-called *H. plicata* are adequate for the designation of a distinct species.

The dichotomous bostryx. A further modification termed a "dichotomy" was recognized as frequent and characteristic of many genera, especially of monocots, and to exemplify this L. and A. Bravais present a drawing of a branch of the inflorescence of "*Hemerocallis fulva*" (the clone Europa). The essential feature of growth in this is that each new unit of the false axis arises directly from the axis of a flower in a dichotomy in the development of which the bracteole, which belongs at the base of the pedicel of the terminal flower, is transposed to a higher level on the false axis. It may be noted that this feature of "dichotomous" branching may also develop in scorpoid cymes. It is to be recognized that the type of branching that occurs in a bostryx of *Hemerocallis* has been designated (Crozier 1892) a helicoid dichotomy or bostrychoid dichotomy as distinct from the true dichotomy seen in Cryptogams. But in *Hemerocallis* branching at a level where there is neither a node nor a bract occurs both in the development of a bostryx and in the precocious separation of axes that lead into bostryxes. The latter will here be called a vegetative dichotomy.

THE BOSTRYXES IN HEMEROCALLIS

The primary bostryxes or terminal inflorescence. The description of the character of a typical bostryx in *Hemerocallis* will here be combined with a consideration of the interrelation of the two or more bostryxes that combine to form the terminal inflorescence. Also the descriptions will first be for the much branched scapes of the species *H. multiflora.* The slender stems and the rather loosely spaced branches in the scapes of this species somewhat simplify the recognition of the essential features of the dichotomous bostryx and the grouping of bostryxes in the primary and the secondary inflorescences.

Figure 17 shows two primary bostryxes which composed a primary inflorescence below which there were secondary inflorescences that are not shown here. The lower one stands as a lateral in the axil of a primary bract (*B1*) on the main axis of the scape. This lateral begins as a single stem and it definitely continues as such for a distance of almost one inch. Then there is a so-called dichotomy, of which one arm continues as a pedicel of a flower while the other is a single vegetative stem as far as the first bracteole (*b1–1*). Above this bracteole the main axis forms another flower stem in which there is a dichotomy. But this second dichotomy of the bostryx is not far above the bracteole (*b1–1*). The next dichotomy, the third of the series, is only slightly above the level of the next bracteole (*b1–2*) and also its two arms stand side by side in a plane almost parallel to that of the base of the bracteole. Thus the lateral in any "dichotomy" does not stand in the axil of the bracteole below it. Each bracteole stands in a position that is opposite to the pedicel



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E. Clarke, del.

of the flower below, a feature emphasized by various writers and especially Goebel (1931). The pedicel of the flower below a bracteole (as *f1–1* in fig. 17), the bracteole (*b1–1*), and the lateral unit of the dichotomy below it are all in the positions relative to each other that they would occupy if there were no displacement. There is, however, much twisting of stem units in the main axis and in the various units of a bostryx which breaks the regularity of alignment.

For the uppermost flower of any bostryx, as shown in figure 17, there is an almost single stem which bears the bracteole (see *b1–3*) belonging to the flower below, and close above, but to one side, there is a much smaller bracteole (see *b1–4*). Immediately in its axil there is the aborted terminal end of the false axis, with often a group of small bracteoles, which is lateral to the pedicel of the last flower.

The upper of two bostryxes in a primary inflorescence terminates the main axis of the scape immediately above the uppermost bract (*B-2* in fig. 17) on this axis. *Its first flower is terminal on the main axis of the entire scape.* A lateral on the axis of this flower arises in a bostrychoid dichotomy and the succession of units in the false axis is like that in the lateral bostryx below.

The terminal bostryx, as a rule, is less developed than the one below; its first flower is smaller than is the first flower of the bostryx below and it opens at least one day later; it frequently has at least one less flower in the series.

The internode between the two upper primary bracts, which subtend the two bostryxes that comprise a primary inflorescence, is often noticeably shortened and frequently the lateral to the lower bract is fused with the main axis (figs. 12, 13). But in the species which have most extensively branched scapes this feature is least strongly developed.

It may here be noted that the spiral phyllotaxy of a bostryx may be either clockwise or counter-clockwise, and that the two primary bostryxes of an inflorescence may both be the same in direction or different.

A three-bostryx primary inflorescence of *H. multiflora* is shown in figure 18. The lower two are laterals on the main axis of the scape; the uppermost one is terminal for this axis. As shown in this figure (at *VD*) a vegetative dichotomy frequently develops in the main axis below the primary bract (between *B2* and *B3* of fig. 18) that subtends the middle one of the three bostryxes. Then the primary bract (*B2*) is carried up on the lateral. Each arm of this dichotomy remains a vegetative stem as far as the next bract. In a dichotomy in the bostryx, however, one arm becomes a pedicel of a

Explanation of figures 17–22

FIGS. 17–22. Scapes of *Hemerocallis multiflora;* figures 17, 18, and 19 are primary inflorescences with 2, 3, and 4 bostryxes; figures 20, 21, and 22 show lateral branches below primary inflorescences.

flower. The precocious separation of a lateral from its main axis is a characteristic feature of growth (a) in the bostryx, (b) in the upper part of the main axis of primary inflorescences, (*c*) in lateral branches of much branched inflorescences (see *VD* in fig. 21), and (d) in at least one species in the first internode (figs. 14, 15) of scapes that are reduced to few flowers.

A four-bostryx primary inflorescence is shown in figure 19. In this there is precocious separation of both the second and the third bostryxes by two successive vegetative dichotomies that occur in the main axis.

The group of primary bostryxes at the apex of a scape constitutes what may be called a primary inflorescence. Occasionally in much branched species there are more than four bostryxes in this group. Always, so it now appears, there are at least two; although in certain species the abortion of one bostryx is frequent in scapes on which only one flower develops to maturity (fig. 16).

The sequence of opening for flowers which occupy corresponding positions in the two or more bostryxes of an inflorescence is almost without exception in succession from the lowest to the uppermost. The dominance in vigor of a lower bostryx to the bostryx above it is conspicuous and almost universal for all inflorescences in all species of *Hemerocallis*. This aspect of growth is also seen when a lateral develops immediately below the terminal in the simpler inflorescence of *H. nana*.

Secondary inflorescences. The secondary inflorescences of *H. multiflora* here shown in figures 20, 21, and 22 exemplify several of the features characteristic of the laterals that develop below the primary inflorescence, especially in species that are rather freely branching. The axis of a secondary inflorescence usually has one or more vegetative internodes for each of which there is a secondary bract (*SB* in figs. 20, 21, and 22). There are usually at least two terminal bostryxes in a secondary inflorescence. The internode between the two bracts may be short (see right branch in fig. 21); it may be quite elongated with the lateral arising in a dichotomy (*D* in fig. 20); or a dichotomy may arise in the main axis below the bract that subtends the first bostryx (*VD* in figs. 14, 15, and 21). In figure 22 is shown a lateral which has a primary inflorescence of two bostryxes below which there is a secondary lateral (to *SB1*) with a dichotomy and two bostryxes. In these the lateral bostryx has only two flowers, and the terminal one has but one flower.

THE INFLORESCENCE OF H. FULVA CLONE EUROPA

The dichotomous bostryx of the Europa daylily was illustrated and described by L. and A. Bravais (fig. 10) and frequently since referred to as exemplifying the "uniparous" helicoid cyme or bostryx. But this illustration is only for a lateral of the two or more bostryxes which form a primary inflorescence. Figure 11 shows a typical two-bostryx inflorescence of this widely cultivated clone at the time when its first flower is ready to open.

Both the dominance in the growth and development of the lateral bostryx and the dichotomous separation of each new lateral segment of the false axis are here well shown. At the conclusion of flowering a two-bostryx inflorescence often appears as in figure 12, and a three-bostryx inflorescence as in figure 13. The interpolation of the axes of the three bostryxes is evident in the segment above the lower primary bract (see *B1*).

In many scapes of plants of this clone only the two or more primary bostryxes are developed and the one or more primary bracts below have no laterals. When there are secondary inflorescences these are placed next below the terminal group of bostryxes and are relatively less strongly developed. The character of the scape of the Europa daylily is quite typical for the species *H. fulva*, which is widely distributed in Asia. In comparison with *H. multiflora* the scapes of the Europa daylily are coarser, and the lateral branches below the primary inflorescence are more often absent or weakly developed.

In the scapes of both *H. fulva* clone Europa and *H. multiflora* it is the rule that there are more than two internodes in the main axis of a scape and that a dichotomy is not seen in the main axis below a primary inflorescence. However in those scapes of *H. minor* which are reduced to only two rather small primary bostryxes there is frequently a vegetative dichotomy in the upper part of the first internode below the level of the first bract (figs. 14, 15).

CONCLUDING REMARKS

The conceptions of the nature of the bostryx or uniparous helicoid cyme, the descriptions of it, and the terms applied to it as presented by the early writers (Schimper according to Braun 1835; and L. and A. Bravais 1837) have been fully endorsed by such later writers on the morphology of inflorescences as Hofmeister (1868), Sachs (1875), Eichler (1875), Bessey (1885), Goebel (1887, 1931), and Velenovsky (1910). Even in the more complicated dichotomous bostryxes, as in *Hemerocallis,* it has been recognized by these authorities that each flower is truly terminal and that the axis of a succession of flowers is composed of a series of false axes each unit of which arises as a lateral. Yet there are recent monographs dealing with the classification of the genus *Hemerocallis* which unreservedly state, without mention of the helicoid and cymose nature of the branches, that the inflorescence is a panicle (Hutchinson 1934) or that its character ranges from racemose to paniculate (Nakai 1932). It is to be noted that the term inflorescence, as well noted by Parkin (1914), is sometimes applied to the mode of floral branching, at other times applied to the flower cluster itself, and at other times it refers to both of these conditions.

In *Hemerocallis,* within each bostryx the flowering is determinate and hence cymose. For the primary group of bostryxes the sequence of development is racemose. This is, evidently, what the term panicle has come to include in the description of the inflorescences in many genera. In *Hemerocallis* the helicoid cyme or bostryx is to be recognized as a unit branch in the inflorescence.

In *Hemerocallis* the consideration of the bostryx refers to the arrangement of flowers in a single flowering branch that may arise in the axil of a bract or terminate a main axis above its last bract. In a bostryx, each flower is terminal for its axis below and its dichotomous lateral continues as a false axis which finally ends in an abortion, and on which the flowering sequence is that of a false raceme.

In all species except *H. nana* two or more bostryxes at the apex of the scape constitute what may be called a primary inflorescence. In the relative development of these bostryxes a lateral one is dominant over the terminal one for the main axis and thus the sequence in the development of these branches is racemose. The same relation in development exists in the group of two or more bostryxes that may terminate any lateral that is below the primary inflorescence.

Thus there is one fundamental feature of growth in the inflorescence that is common to all the species of *Hemerocallis*. In *H. nana* many scapes have two flowers, one terminal on the main axis and one terminal on a lateral, and in all other species at least two bostryxes combine to form a terminal inflorescence. In both cases the lateral dominates in size, vigor of growth, and time of development. The flowering of the central or main axis and of the laterals is determinate and the sequence of development is centripetal. It is the development of branches from the pedicels, in all species except *H. nana*, and their precocious separation by dichotomy that give the false axis and the racemose appearance of the bostryx in *Hemerocallis*.

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THE ONTOGENETIC DEVELOPMENT AND PHYLOGENETIC SPECIALIZATION OF RAYS IN THE XYLEM OF DICOTYLEDONS—III. THE ELIMINATION OF RAYS[1]

ELSO S. BARGHOORN, JR.

(WITH FOURTEEN FIGURES)

Extensive study[2] of the ontogeny and phylogenetic specialization of rays reveals that ray tissue may be completely eliminated from the secondary xylem. The process of ray elimination is not an isolated phenomenon, but occurs in a wide range of dicotyledonous shrubs and semi-shrubs. The absence of rays is correlated with reduction in cambial activity and often with a tendency toward the herbaceous habit of growth. In addition, the rayless condition occurs in many shrubs and suffruticose forms possessing anomalous secondary thickening, included phloem, successive cambia, etc. A conspicuous suppression, though rarely complete absence, of rays may be observed in many plants which have undergone dwarfing or modifications in relation to xerophytic or otherwise unfavorable environments. The various ontogenetic changes which effect the elimination of rays are emphasized in this study; in addition, however, the relation of ontogeny to phylogeny is considered.

Kribs' investigations on the structural specialization of rays in dicotyledons do not include data on the elimination of rays (Kribs 1935). However, from previous studies by the writer (Barghoorn 1940, 1941) it is evident that the loss of rays results in a highly specialized condition. Additional evidence for this is afforded by the fact that rayless structure occurs in a wide range of unrelated families (figs. 1–6, 7, 9, 10), and is usually associated with a high degree of general structural specialization.

From Kribs' study, supported by the writer's investigations, there are two major trends of specialization of ray tissue in dicotyledons. These are the elimination of uniseriate rays to leave multiseriate rays only, and the elimination of multiseriates to leave uniseriates only. Both of these trends are usually associated with changes in the morphology of the ray cells. In the rayless forms and those with poorly developed rays the tendency towards the elimination of both types of rays coincides with the reduction in secondary growth. It has been shown in earlier papers of this series that phylogenetic modification of ray structure may be initiated in either the early or the later stages of ontogeny of the secondary body. In the elimination or extreme reduction of rays, however, phylogenetic specialization proceeds from the early to the later stages of development rather than vice-versa. That is, phylogenetically the rays are lost from the inner secondary xylem before their elimination from the outer parts of the secondary body. This is indicated by the fact that in many shrubs and semi-shrubs rays are absent from the inner portions of the woody cylinder while present in varying numbers in the outer portions (figs. 7, 8). No well developed rays have been observed in the inner secondary xylem of species devoid of rays in the outer. Moreover, frequently the vestiges or "ghosts" of rays may be observed in transverse sections, while radial or tangential longitudinal sections show conclusively that rays are absent (figs. 1, 2, 3, 9). From these facts it is quite clear that the elimination of ray tissue is a morphological modification which is the reverse of the so-called recapitulation phenomenon. This is evidenced by the fact that the ancestral condition, viz., the presence of rays, is represented in the later stages of development rather than in the early stages.

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[1] The first paper of this series appeared in Am. Jour. Bot. 27: 918–928. 1940. The second paper will appear in Am. Jour. Bot. for April, 1941.

[2] In this series of investigations various species from 195 families of dicotyledons were examined from the extensive slide and wood collections of Harvard University.

From the standpoint of ontogenetic development the phylogenetic specialization of rays is accomplished by a consecutive series of increasingly modified ontogenies. In the loss of rays the tendency for elimination is expressed, ontogenetically, at increasingly later stages of development until eventually the secondary xylem is entirely devoid of rays. Various stages in the ontogenetic-phylogenetic elimination of rays are similar in clearly unrelated groups of dicotyledons. They therefore represent similar, parallel trends of phylogenetic specialization brought about by similar ontogenetic changes.

THE ELIMINATION OF RAYS BY THE ENLARGEMENT OF RAY INITIALS

Various complex cellular changes characterize the development of rays in the cambium (Chattaway 1933, Barghoorn 1940, 1941). Among these is the transformation or reversion of ray initials to the fusiform type of cambial cell. If such a transition is localized and definitely oriented within a multiseriate ray the elongating initials split or dissect the ray into two or more separate portions as illustrated in figure 7 of the second paper of this series. If, however, the tendency for elongation affects all the ray initials, the ray tends to lose its distinct morphological identity, since its constituent cells may resemble in size and shape the cells of the surrounding tissue (figs. 8, 11). For the sake of completeness it should be pointed out that ontogenetically such extensive change in all the initials of a ray seldom occurs during development of the secondary xylem of an individual. If a phylogenetic series is studied, however, it becomes clear that the degree of emphasis on ray initial elongation, at different stages, results in the partial or complete elimination of the rays as distinct structures.

The majority of species in which rays are in course of elimination by the enlargement of initials do not possess uniseriate rays. In these, therefore, the

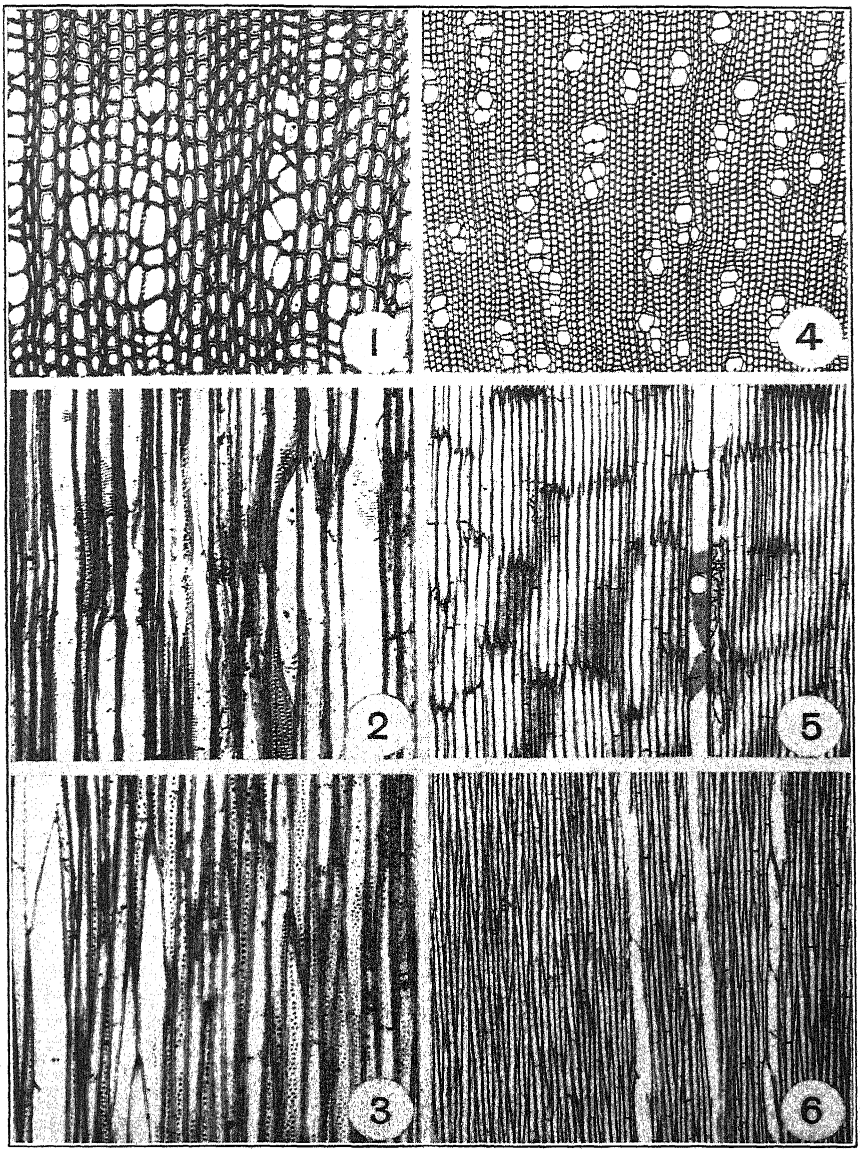


FIG. 1. *Alseuosmia macrophylla* Cunn. (Caprifoliaceae). Transverse section of the secondary xylem. Note the absence of rays. The radial rows of smaller cells represent the "ghosts" of rays which have been eliminated (×125). FIG. 2. *Alseuosmia macrophylla.* Radial longitudinal section indicating, similarly, the absence of rays (×125). FIG. 3. *Alseuosmia macrophylla.* Tangential longitudinal section showing the rayless secondary xylem. Compare with figs. 1 and 2 (×125). FIG. 4. *Besleria* sp. (Gesneriaceae). Transverse section showing secondary xylem completely devoid of rays. In this species wood parenchyma is nearly absent and the secondary xylem consists almost entirely of vessels, libriform fibers, and septate fibers (×40). FIG. 5. *Besleria* sp. Radial longitudinal section showing the rayless secondary xylem in longitudinal view (×40). FIG. 6. *Besleria* sp. Tangential longitudinal section. Note the complete absence of rays. Compare with figs. 4 and 5 (×40).

majority of the ray tissue consists of heterogeneous multiseriate rays of varying size, composed of large, more or less vertically elongated cells, as shown in figures 8 and 11. Occasionally uniseriate rays are present as well, but these are likewise composed of vertically elongated cells. Heterogeneous multiseriate rays such as occur in the early stages of the elimination of rays should not be confused with the heterogeneous multiseriates of the primitive ray structure. The specialized multiseriate rays occur in species which usually exhibit a high degree of structural specialization of the secondary xylem. Their cells frequently appear irregular and angular when viewed in tangential longitudinal sections and commonly possess thin secondary walls which are devoid of the abundant, conspicuous, simple pitting found in primitive multiseriate rays (fig. 11).

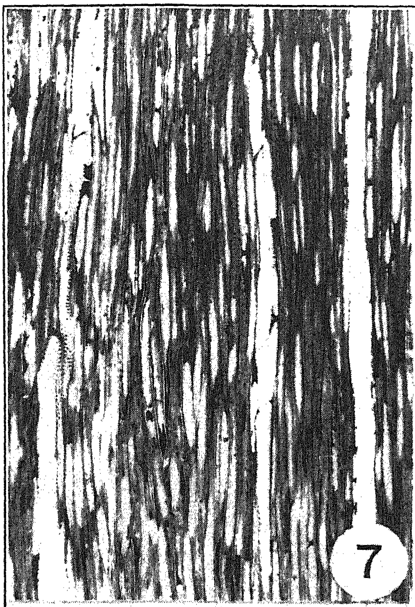
Interestingly enough, the phylogenetic elimination of rays by the progressive increase in the size of ray initials brings about their loss by expansion rather than reduction. In other words the rays are eliminated by the "overdevelopment" rather than suppression of their initials.

REDUCTION OF RAYS BY THE SUPPRESSION OF RAY INITIALS

In strong contrast to the elimination of rays by the enlargement of their initials is the reduction of ray tissue by the suppression of ray initials in the cambium. As has been previously noted, this condition is found chiefly in dwarfed plants, of suffruticose habit, growing in xerophytic or otherwise unfavorable environments. Not only is cambial activity reduced in such plants but the size of the cambial initials is often reduced far more than would be anticipated from the degree of phylogenetic specialization of the vessel elements. Shrubby forms such as these therefore exhibit strong tendencies toward similar anatomical modifications even though they may differ widely in the extent of structural specialization of the secondary xylem, or in their floral morphology.

Explanation of figures 7–10

FIG. 7. *Geranium tridens* Hbd. (Geraniaceae). Tangential longitudinal section of inner secondary xylem indicating the absence of rays in the early stages of development of the secondary xylem. Phylogenetically the ray initials in the early stages have elongated to the fusiform type of cambial cell (×95). FIG. 8. *Geranium tridens.* Tangential longitudinal section of outer secondary xylem of same stem indicating the presence of high-celled multiseriate rays in the later-formed secondary xylem. Phylogenetic modification has not yet resulted in the elimination of rays in the later stages of development of the secondary xylem (×95). FIG. 9. *Sempervivum arboreum* L. (Crassulaceae). Transverse section showing portions of the pith and the rayless early secondary xylem. Note the "ghosts" of multiseriate rays extending outward from the pith. Tangential and radial longitudinal sections show that the woody cylinder is completely devoid of rays (×95). FIG. 10. *Frankenia grandiflora* Ch. and Schl. (Frankeniaceae). Transverse section of secondary xylem of a root showing secondary thickening by means of successive cambia. Note the complete absence of rays, a condition characteristic of this type of structure (×95).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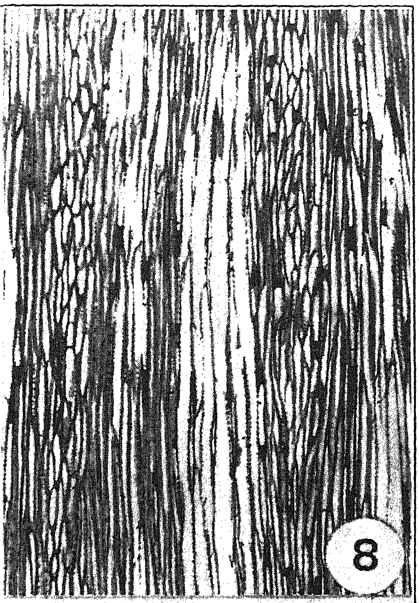
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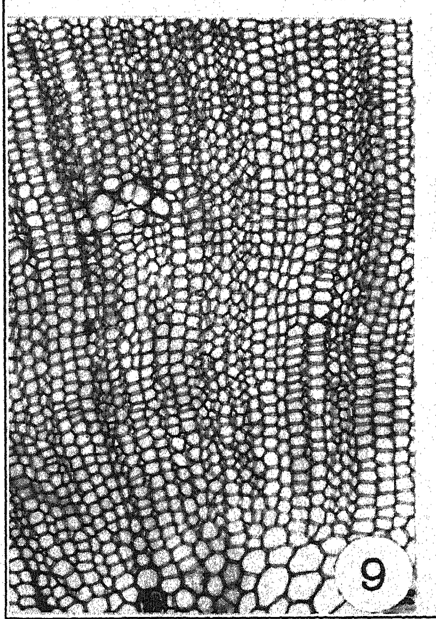
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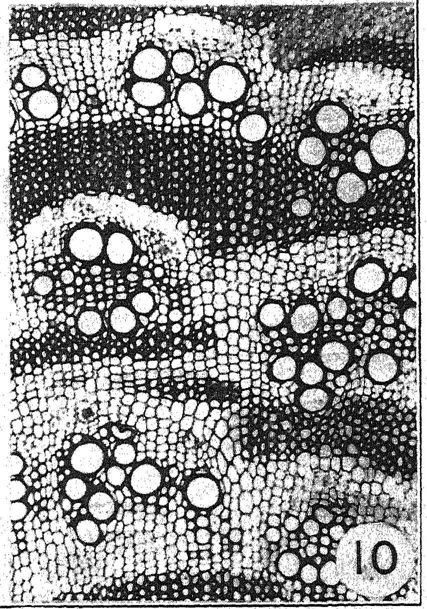
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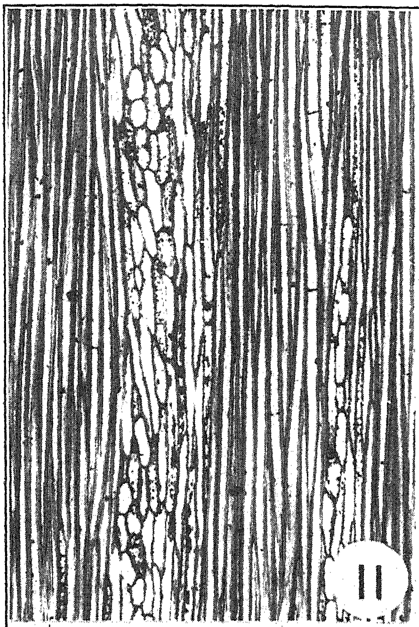
The influence of dwarfing on the ray tissue of the secondary xylem usually affects the height and width as well as the number of rays (Forsaith 1920). Commonly the multiseriate rays are eliminated and the uniseriate rays reduced in height (figs. 13, 14). Frequently the uniseriate rays are composed of vertically elongated cells only (figs. 12, 13, 14). Further reduction of the ray tissue tends to produce rays extended by solitary initials or by uniseriate strands of initials from three to four cells high. In extreme cases of reduction the xylem ray cells are somewhat disjunctive and therefore not radially contiguous. In certain members of the Cistaceae the innermost secondary xylem is devoid of rays while the outer parts possess only one-celled uniseriate rays of the disjunctive type.

As in the elimination of rays by cell enlargement, the tendency for suppression of rays affects first the early stages of secondary growth. This is apparently true regardless of the degree of structural specialization of the xylem or the extent to which the ray tissue is reduced. Thus in many species the multiseriate rays have been eliminated from the inner secondary xylem leaving high-celled uniseriates only, whereas in the outer secondary xylem both multiseriate and uniseriate rays are present. Similarly, if only reduced uniseriate rays are formed throughout the secondary xylem, they are frequently less numerous in the early stages of development and composed of cells which are more elongated vertically than ray cells in the later stages.

It should be emphasized that in the elimination or reduction of rays there is not a phylogenetic trend from heterogeneity to homogeneity. Rather, the reverse is true, particularly of rays being eliminated by cell enlargement, inasmuch as ray initials and their daughter cells progressively increase in the vertical dimension instead of becoming more nearly isodiametric. The anatomical modifications which characterize the reduction or elimination of rays are identical in both roots and stems. There is no significant difference in the ontogeny or the rate of phylogenetic specialization of ray tissue in the two major portions of the plant.

Explanation of figures 11–14

FIG. 11. *Ardisia Brackenridgei* (A. Gray) Mez. (Myrsinaceae). Tangential longitudinal section of secondary xylem showing the tendency to loss of rays by the vertical elongation of ray initials. (×95). FIG. 12. *Staavia glutinosa* (l.) Thbg. (Bruniaceae). Tangential longitudinal section illustrating the tendency to reduction of rays by suppression of them in the cambium. Multiseriate rays have been eliminated and the uniseriate rays are composed solely of vertically elongated cells (×95). FIG. 13. *Corema Conradii* Torr. (Empetraceae). Tangential longitudinal section showing marked reduction of ray tissue. Note that many of the rays are reduced to the one-celled uniseriate condition (×230). FIG. 14. *Tetratheca ciliata* Lindl. (Tremandraceae). Tangential longitudinal section illustrating reduction of ray tissue similar to that shown in figs. 12 and 13. The plants represented in figs. 12, 13, and 14 all exhibit conspicuous morphological as well as anatomical reduction (×95).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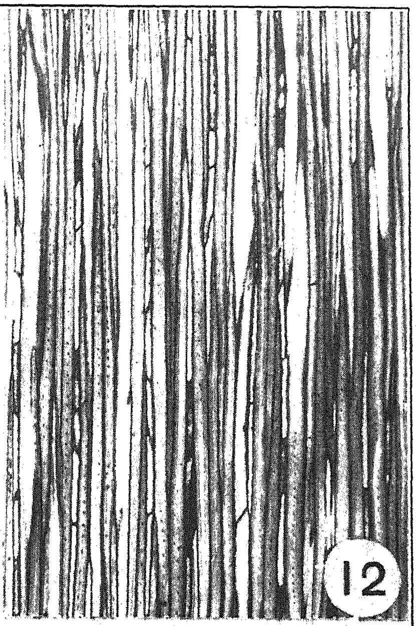
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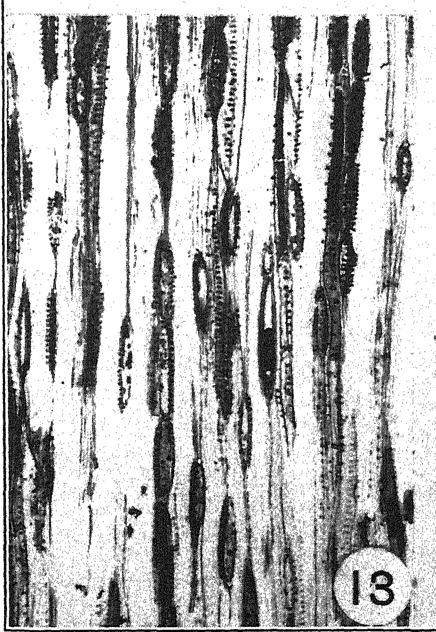
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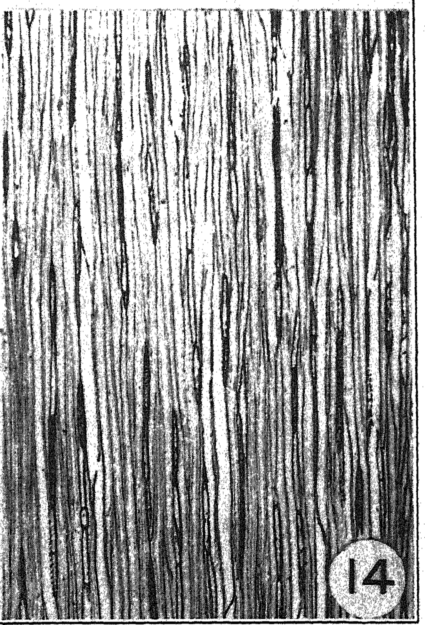
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ANOMALOUS SECONDARY GROWTH AND THE LOSS OF RAYS

In many species of dicotyledons, particularly in the Centrospermae, secondary thickening occurs by the activity of successive cambia. In such plants, particularly if secondary growth is rather limited, the woody cylinder is commonly devoid of ray tissue (fig. 10). In some species, in the innermost secondary xylem, and before the formation of supplementary cambia, rather poorly defined, high-celled multiseriate rays may be developed. These, however, are not continuous across the arcs of included phloem which are subsequently formed. Similarly, in the broader zones of uninterrupted secondary xylem of later stages, high-celled multiseriate rays may be produced, but these too are transitory and therefore do not constitute normal ray tissue.

It is quite clear that the formation of successive cambia and included phloem is not a stage in the phylogenetic modification of rays. However, it is an anatomical modification which is closely associated with a loss of ray tissue and commonly results in the complete elimination of rays.

SUMMARY

1. Extensive study of the anatomy of dicotyledons reveals the fact that ray tissue may be completely eliminated from the secondary xylem.

2. The absence of rays is a highly specialized condition, associated with reduction of cambial activity and in many cases with a tendency toward the herbaceous habit of growth. The rayless condition also occurs in many plants possessing anomalous secondary thickening.

3. The elimination of rays is accomplished phylogenetically by the transformation of ray initials to fusiform initials.

4. Conspicuous reduction, though rarely complete absence of rays may result in plants which have undergone dwarfing or extensive modifications in relation to xerophytic or otherwise unfavorable environments. In these cases the formation of ray initials is suppressed in the cambium.

5. Phylogenetically, the elimination of rays is initiated in the early rather than in the later stages of development of the secondary xylem. The tendency for loss of rays is extended, phylogenetically, into successively later stages of ontogeny until the woody cylinder is devoid of ray tissue.

The writer wishes to express his appreciation to Professor I. W. Bailey for his interest and assistance in this study.

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NOTES ON APHANIZOMENON WITH A DESCRIPTION OF A NEW SPECIES[1]

Edward G. Reinhard[2]

(WITH FIVE FIGURES)

Aphanizomenon is a familiar blue-green alga common in the plankton of quiet waters, often forming a heavy bloom on the surface of ponds and lakes during the summer and early autumn. Its plate-like bundles of agglutinated trichomes are very noticeable to the unaided eye, appearing like small bits of cut grass.

Only a single species, *Aphanizomenon Flos-aquae* (L.) Ralfs, has heretofore been reported from the United States. This alga is so abundant at times that it dominates the plankton and gives the water a semblance of green paint. In a bay at the eastern end of Lake Sakatah in southern Minnesota the writer observed a vast mass of *Aphanizomenon*, probably concentrated by the wind. The water contained *Aphanizomenon* filaments to the number of 2,500,000 per cc. Associated with this species were colonies of *Microcystis aeruginosa* Kuetz. numbering 600 per cc. This dense population of algae increased the dissolved oxygen content of the water to supersaturation on October 15, 1929, when this observation was made; the water temperature was 22° C.

The generic description of *Aphanizomenon* given by most phycologists includes the statement that the spores (akinetes) are solitary. Yet Schmidle (1897) described a species possessing 1–3 spores in series. This species, which he called *Aphanizomenon Kaufmanni*, is recognized as a true representative of the genus, but phycologists in general have neglected to revise the generic description to include the species with seriate spores.

This neglect was mainly due to the fact that the description of the new species remained virtually unknown for a long time after publication, no doubt because it was incorporated in an article by P. Kaufmann which appeared in an obscure publication, *Revue d' Égypte*, a publication which is now almost inaccessible. In 1914, however, Brunnthaler in *Hedwigia* brought Kaufmann's article to the attention of botanists by publishing a brief abstract of it and reprinting Schmidle's Latin diagnosis of the species together with the original figures. The species is also described, but not figured, by Geitler (1925). It is one of the organisms chiefly responsible for the so-called "green water," an annual phenomenon of the Nile.

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[1] Contribution from the Department of Biology, The Catholic University of America, Washington, D. C.

[2] The author is indebted to Prof. J. E. Tilden for assistance in this study, which was begun in the Botanical Laboratories of the University of Minnesota.

While investigating the plankton of the upper Mississippi River and its tributaries (Reinhard 1931), I came upon an *Aphanizomenon* which is strikingly different from *A. Flos-aquae* and resembles the species which Schmidle described from the Nile. It appeared in the plankton of the Minnesota River and was so abundant that it imparted to the concentrated plankton sediment a very noticeable blue-green color, which was even apparent, though much less distinct, in the unconcentrated water. The sample from the Minnesota River was taken at Mendota on July 31, 1928, from a depth of five feet in mid-channel. This species was found in association with other algae as follows:

Aphanizomenon sp. nov.	22,200	individuals	per	cc.
Melosira granulata	186	"	"	"
Gyrosigma Spenceri	42	"	"	"
Green flagellates	96	"	"	"

In the Mississippi River likewise, below its confluence with the Minnesota, this *Aphanizomenon* was present in the plankton as far down as the head of Lake Pepin. Above the Minnesota it did not occur at all. The numbers, however, progressively diminished in the Mississippi water, and it is apparent that the *Aphanizomenon* originated and developed in the Minnesota and was contributed to the Mississippi plankton by the tributary water.

The Minnesota is a broad, slow-moving stream with scarcely any slope in the last fifty miles of its course. It occupies a wide valley, the bottom lands marshy and fringed with ponds. It is probable that the *Aphanizomenon* originated in these marshes.

The month of July was a period of relatively low water with high temperatures. During this period the temperature of the Minnesota River was 26° C., the warmest record for the year.

Like the *Aphanizomenon* of the Nile, the Minnesota species was short-lived as a plankton constituent. The following table gives the only occurrences of this peculiar species throughout the 1928 plankton investigation, although collections were made every two weeks from February to October.

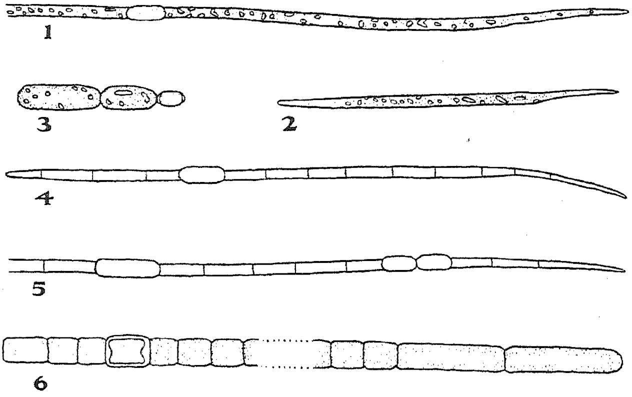
TABLE 1

Stations	Miles below Minnesota River	Date	Water temperature °C.	*Aphanizomenon* filaments per cc.
Minnesota River at mouth	0	July 31	23	22,200
Mississippi R. at Inver Grove	15	July 31	23	1,200
Mississippi R. at Hastings	33	Aug. 2	22	530
Mississippi R. at Red Wing	55	Aug. 1	24	465

This alga, allied to *A. Kaufmanni,* appears to be a new species. I propose to name it *Aphanizomenon americanum,* since it is the first species of *Aphanizomenon* to be described from the United States.

Aphanizomenon americanum Reinhard, sp. nov. Filamentis solitariis aut in laminulis tenuiter inter se coniunctis, rectis aut quasi curvatis vel prope sigmoideis, aerugineis, ad 200 μ longis, ad disseptimentes vix visibiles non constrictis; trichomatibus ad unum aut utrumque apicem elongatis quasi caudatis; apicibus ex 1–3 cellulis tenuibus formatis, cellulis apicalibus ad 16 μ longis, cellulis vegetativis cylindricis, 2–3 μ latis, 6–13 μ longis, pseudovacuolis rubris. Sporis singulis aut duobus contiguis, elongatis, fere cylindricis et utrimque rotundatis, 3–5 μ latis, 6–13 μ longis, intus quasi granulosis. Heterocysta (solam unam vidi) longe elliptica, 2.6 μ lata, 3.5 μ longa, sporis proxima.

Plant mass floating; trichomes 100–200 μ in length, solitary or loosely united in thin plate-like bundles, straight, slightly curved or nearly sigmoid, tapering at one or both ends into caudate extensions of 1–3 apical cells, not constricted at the joints, blue-green in color with reddish pseudovacuoles. Vegetative cells cylindrical, 2–3 μ in diameter, 6–13 μ in length, narrowed apical cell sometimes reaching a length of 16 μ. Akinetes 3–5 μ in diameter, 6–13 μ in length, single or geminate, subcylindrical, elongate, rounded at both ends; cell contents granular. Heterocyst (I have seen but one) 2.6 μ in diameter, 3.5 μ in length, somewhat elliptical, situated adjacent to the akinete.



FIGS. 1–5, *Aphanizomenon americanum* Reinhard. FIG. 6, *Aphanizomenon Flos-aquae* (L.) Ralfs, drawn to same scale for comparison. All × 900. FIG. 1, typical appearance of trichome. FIG. 2, young sterile trichome. FIG. 3, two large akinetes with a heterocyst above. FIGS. 4, 5, trichomes with akinetes, drawn to show cell walls.

A comparison between Schmidle's description of the *Aphanizomenon* of the Nile and the description which I have just given of the Minnesota plant does not appear at first glance to bring out any clear-cut distinctions between the two. This is partially due to the limitations of language and to the brevity of the earlier description. But if the drawings of the two forms are used to illustrate the meanings of the words employed it becomes evident at once that significant differences do exist. Only an exact comparison of actual specimens can, of course, positively demonstrate every point of dissimilarity.

Aphanizomenon americanum appears to differ from *A. Kaufmanni* Schmidle in the following respects:

A. Kaufmanni	*A. americanum*
One attenuated apical cell.	A series of attenuated cells at the apices.
Apices sometimes twisted spirally.	Apices always straight.
Length of heterocyst at least twice the diameter.	Length of heterocyst less than twice the diameter.
Akinetes somewhat elliptical.	Akinetes with sides practically parallel.

The septa separating the cells of *A. americanum* are not discernible unless special methods are employed to demonstrate them. Staining the trichomes with an aqueous solution of neutral red works well on material preserved in formalin and brings out the transverse septa very clearly.

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A NEW CYPERACEOUS GENUS FROM NORTHERN SOUTH AMERICA

Charles Gilly

Floristic and taxonomic studies have revealed the presence of a great number of endemic genera in the Sierra Pacaraima, an ancient mountain complex along the Venezuela–Brazil–British Guiana boundary. The botanical collections of Mr. G. H. H. Tate from Mt. Roraima, Mt. Duida, and Mt. Auyan-tepui have been the basis for the description of many of these endemics. Among his collections were specimens of dioecious Cyperaceae which are here recognized as an addition to the list of endemic genera of this area. Dioecism, of itself, cannot of course be regarded as a generic character in the Cyperaceae, but dioecism together with a sufficient number of habital characters can serve as an indicator of generic difference.

Böckler (1) in 1874 described *Cryptangium stellatum* on the basis of a pistillate plant, *Schomburgk 1227,* from British Guiana; the exact collection locality of this specimen is not given, but it quite certainly is somewhere near Mt. Roraima. *C. stellatum* differed from other members of the genus not so much in its dioecious character, for there were already other known dioecious species of *Cryptangium,* as by the arrangement of its leaves and inflorescence. The staminate plant of the species was described in 1886 by Ridley (5); both Ridley's description and the figure which appeared in 1887 (7) were based on *im Thurn 357* from Mt. Roraima. Ule also collected staminate plants from Mt. Roraima (6), and I have previously reported (3) the staminate collection made by Tate on Mt. Auyan-tepui. Among the specimens referred to the genus "*Everhardia*" by Britton in the Duida report (2) was *Tate 542,* which I have already excluded from *Everardia* (4); comparison of this specimen with the Tate specimens of *Cryptangium stellatum* from Mt. Auyan-tepui leaves little doubt that, despite their superficial dissimilarity, they are congeneric. Inasmuch as I am convinced that they represent a separate genus, distinct from and not at all closely related to *Cryptangium,* I propose for them the following name:

DIDYMIANDRUM[1] GILLY, GEN. NOV.

Herba perenna terrestris vel epiphytica dioica; culmi rhizomati lignosi erecti triangulares; folia conferta subverticillatim terna disposita persistentia; vaginae rigidae truncatae; inflorescentia multipaniculata multiramosa multispiculata interrupta, paniculae singulares in tertia quaque axilla; spiculae masculae geminae vel rare solitariae vel tres simul, glumis

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[1] Derived from two Greek words meaning *twin* and *male,* in reference to the usually paired staminate spikelets.

exterioribus vacuis 5–8, glumis interioribus fertilibus 2–8; stamina a gluma fertili subtenta 2–3, filamentis persistentibus; spiculae foemineae 1-florae solitariae vel rare geminae, glumis 5–?; achaenium triangularium tricostatum apice rostrato; perianthio trifido, lobis bifidis ciliolatis; stylo trifido.

Type species: *Cryptangium stellatum* Böckl.

Didymiandrum is most closely related to the genera *Everardia* and *Cephalocarpus*, both of which are Sierra Pacaraiman endemics, and with them is referable to the tribe Lagenocarpeae.[2] *Didymiandrum* may be most easily separated from these other two genera by its dioecious inflorescence and the subverticillate arrangement of its leaves.

KEY TO THE SPECIES[3]

Leaves lanceolate to lanceolate-elliptic, 5–18 cm. long, 2.5–4 cm. wide, either entirely glabrous or glabrous except for the white-ciliate margins .... 1. *D. stellatum*

Leaves narrowly linear, 15–25 cm. long, 1.5 mm. or less in width, minutely soft-pubescent on both surfaces .... 2. *D. flexifolium*

1. **Didymiandrum stellatum** (Böckl.) Gilly, comb. nov. *Cryptangium stellatum* Böckl. Linnaea **38**: 421. (descr. plantae ♀). 1874; descr. ampl. Ridley, in im Thurn, Timehri **5**: 209. (descr. plantae ♂). 1886. *Acrocarpus stellatus* Nees; Böckl. Linnaea **38**: 421 (in synonymy). 1874. *Lagenocarpus stellatus* (Böckl.) Kuntze, Rev. Gen. 754. 1891.

Culmi stricti ad 1 m. alti; folia lanceolato-elliptica vel lanceolata plana omnino glabra vel glabra praeter margines ciliolatos, 5–18 cm. longa, 2.5–4 cm. lata; culmus quisque floriferus multiramosus, cum inflorescentia ad 20 cm. altus; spiculae masculae ad 6 mm. longae, glumis vacuis 6–8 ovatis vel lanceolatis mucronatis 1–2 mm. longis, glumis fertilibus 2–4 lanceolatis acutis vel acuminatis ad 4 mm. longis; spiculae foemineae subturbinatae ad 3–4 mm. longae, glumis 5 ovatis inferioribus cuspidatis superioribus mucronatis; achaenium obtuse triangulare tricostatum ad basim obovatum, apice rostrato attenuato subtruncato; perianthio trifido, squamis bifidis ciliolatis; stylo brevi, stigmatibus 3.

Specimens examined: Venezuela–Bolivar: Mt. Auyan-tepui, 2200 m., Dec. 1937, *Tate 1348* (NY). Also reported (5, 6, 7) from Mt. Roraima.

2. **Didymiandrum flexifolium** Gilly, sp. nov. Planta mascula: Rhizomati ad 3 mm. diam. et 30 cm. alti; folia linearia acuta persistentia pubescentia plana praeter apicem bicarinatum, 15–25 cm. longa, 1.5 mm. minusve lata; culmus quisque floriferus rigidus erectus, cum inflorescentia 5–15 cm. altus; spiculae masculae 5 mm. longae, glumis vacuis 5 ovatis subbifidis mucronatis ad 1 mm. longis, glumis fertilibus 6–8 lanceolatis acutis 4–5 mm. longis. Planta foemina et achaenium ignota.

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[2] This tribe is usually called the Cryptangiae, but because of the doubtful status of the genus *Cryptangium* I am following Pfeiffer in the choice of a tribal name.

[3] Specimens examined in this study are deposited in the herbarium of the New York Botanical Garden (NY), and in the United States National Herbarium at Washington, D. C. (US).

Specimens examined: VENEZUELA—TERRITORIO AMAZONAS: Mt. Duida, epiphytic on bark of tree, flat near stream at Central Camp, 4800 ft., Dec. 20–28, 1928, *Tate 542* (NY, TYPE; US).

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Papers that relate exclusively to bacteriology, forestry, agriculture, horticulture, manufactured products of vegetable origin, or laboratory methods are not included. If users of the Index will call the attention of the editor to errors or omissions, their kindness will be appreciated.

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COMPARATIVE STUDIES ON THE STRUCTURE OF THE SHOOT APEX IN SEED PLANTS[1]

ADRIANCE S. FOSTER

(WITH FOUR FIGURES)

INTRODUCTION

In common with other vascular plants, the typical sporophyte of the seed plants has the ability to produce, throughout its growing periods, a succession of organs and tissues on a theoretically unlimited scheme. This method of development is possible first of all because small areas of dividing and enlarging cells, localized at the apices of shoots and roots, are permanently maintained in a state of potential activity. From these embryonic areas, which are designated as terminal meristems, there arise the primordia of foliar organs and the "primary tissues" of the stem and root.

Following the classical researches on apical growth made by Nägeli during the middle of the last century, much labor was devoted to the study and interpretation of structure and growth in terminal meristems. In particular, the meristematic apex of the shoot, because of its dual role as the initiator of appendages and the primary tissues of the axis, attracted considerable attention. Among the celebrated botanists who contributed to a knowledge of the shoot apex may be mentioned Hofmeister (1857), Hanstein (1868), Pringsheim (1869), Strasburger (1872), Sachs (1878), Haberlandt (1880), and Schwendener (1879, 1885). It is not my intention to review at this time these early pioneering studies, since the details are adequately presented in Schüepp's (1926) monograph on meristems as well as in a recent historical résumé by the writer (Foster 1939b). It is necessary, however, to emphasize that the structural picture of the apex which emerged from most of these studies was that of a complex network of cell walls (cf. especially Sachs 1878). This highly formalized and "lifeless" representation of the cellular structure of the apical meristem resulted in the first place from the crude microtechnique then in vogue, which consisted in the treatment of

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[1] Invitation paper read before Section G of the A.A.A.S. at the Philadelphia Meeting on December 28, 1940. It is a pleasure to thank my wife for her assistance in preparing the drawings made to illustrate this paper.

[THE BULLETIN FOR MAY (68: 265–338) WAS ISSUED MAY 1, 1941]

hand sections with Eau de Javelle or KOH in order to remove completely all protoplasm. But aside from the limitations imposed by technique, great importance was attached to the details of the cell-wall mosaic because of efforts to determine the exact origin of cells either from a single definitive apical cell or from a series of initials. From this standpoint, one of the chief objectives of inquiry in the study of the shoot apex was the plan of cell arrangement with reference to the initials. This could be vividly described and depicted in terms of an intersecting network of cell walls.

The unfortunate result of this restricted form of inquiry was that the larger questions of the cellular organization and activity in the apex as a whole and the nature of its relation to growth and differentiation in the shoot continued to be neglected. Hanstein's (1868) histogen theory, it is true, seemed at first to provide a solution to the problem of tissue differentiation in the stem and root. But the careful studies of Koch (1891, 1893) and Schoute (1903) among others, during the latter part of the 19th century, demonstrated the impossibility of recognizing a rigid correspondence between specific cell layers in the apex and the origin of leaves and the primary tissue systems of the shoot axis (cf. also Foster 1939b). This idea has been further supported by an intensive study within recent years of apical ontogeny in the shoots of certain periclinal chimaeras (Lange 1927). It seems clear from this work that, with respect to the number of generative layers involved, there is no uniform scheme of bud and leaf initiation in the angiosperms investigated and that the problems of tissue and organ determination are not to be solved by a theory of specific histogens (Foster 1936, Jones 1937). Indeed F. O. Bower (1935, p. 328), whose early studies on the terminal meristems of ferns are a classic in morphology, has reached the conclusion that "on the one hand apical segmentation, and on the other morphological definition, whether external or internal are distinct processes, each of which is determined by the apical region as a whole, and not by its segments."

The above quotation from Bower serves to show the unsatisfactory state of our knowledge of the role of the shoot apex in the differentiation process. We must admit, I think, that the continued emphasis merely on the formal questions of cell origin and cell arrangement in apical meristems holds little or no promise of furnishing additional insight into this fundamental problem. What is needed is a more realistic approach, utilizing the advantages of modern botanical technique in an effort to study all possible aspects of cell structure and cell activity rather than simply the mosaic of cell walls.

The purpose of this paper is to describe the most significant results of certain very recent cyto-histological studies on the shoot apex of seed plants. One of the most interesting aspects of these exploratory studies is the demonstration that the so-called "primordial meristem" of the apex varies considerably in its structure in different plants and that it should no longer be regarded simply as an "undifferentiated" or homogeneous tissue as is done by such authors as Haberlandt (1914, p. 73). On the contrary, the apical meristem is segregated into more or less well-defined *tissue zones.* These zones are distinguished from each other by such features as cell size, nuclear size, planes of cell division, relative frequency of mitosis, reaction to plasma and nuclear stains, and relative thickness of cell walls. As I shall show in describing the various types of zonal patterns, this structural diversity in the so-called primordial meristem is not only interesting from the standpoint of comparative anatomy but also appears to throw new and important light upon the nature of organ and tissue differentiation. For convenience and emphasis, the observations will be separately described under the main groups of gymnosperms and angiosperms which have been examined from the new point of approach.

GYMNOSPERMS

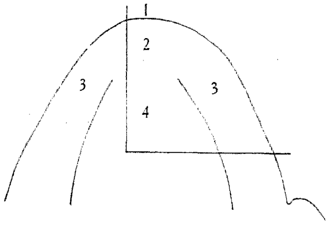
Recent investigations have revealed a number of interesting types of zonal structure in the shoot apex of the gymnosperms. Since the limitations of space do not permit of a detailed contrast between the various types of zonal patterns, I shall attempt to summarize only the most significant of the new facts.

Coniferales. The apex of *Abies venusta* (Dougl.) K. Koch illustrates a zonal pattern which is apparently wide-spread in the conifers (Koch 1891, Korody 1937, Cross 1939, Foster 1939a). In this type, the tissue of the apex is segregated into two well-defined zones, viz.: an outer *peripheral zone* of deeply-stained, actively-dividing cells from which ultimately arise the leaf primordia as well as the epidermis, cortex, and provascular tissue; and an inner core or *central-tissue zone*, composed of filamentous groups of highly-vacuolate elongating and dividing cells, which is the precursor of the pith (fig. 1). Both of these zones originate from a small ill-defined subterminal group of "mother cells" which in turn have arisen from the inner derivatives of the apical initials (fig. 1a). Except for a more regular surface cell layer, this zonal pattern is duplicated fundamentally in the apex of *Araucaria Bidwilli* Hook., and Cross (1939) has recently described a similar type of zonal structure for the apical meristem of the shoot of *Taxodium distichum* (L.) Rich. One of the most significant features of this type of apical structure is the inequality between the two zones with respect to the *relative rates* of cell division, cell enlargement, and cell maturation. The *central tissue zone* is typified by the polarized growth and the rapid progressive elongation of the cells from their point of origin. In contrast, the *peripheral zone* exhibits less evidence of early specialization and appears to consist of a rather uniform tissue in which cell division rather than cell enlargement predominates. Further consideration of the implication of these differences will be deferred until other types of zonal structure have been described.

Ginkgoales and Cycadales. As representatives of the two most primitive groups of living seed-bearing plants, *Ginkgo* and the cycads have naturally attracted much morphological study and speculation. But it is only within the last two years that information has appeared regarding the cyto-histology of the shoot apex of these archaic seed plants. A priori, it might be assumed that the so-called "primordial meristem" of the apices of these ancient spermatophytes would be simple and undifferentiated in structure. On the contrary, the apical meristem exhibits, in a very impressive way, a distinct and complex type of zonation.

In *Ginkgo* (Foster 1938) the apices of both spur and long shoots are fundamentally similar in zonal structure. The most distinctive feature is furnished by the *central mother-cell zone* which consists of a well-demarcated cup-shaped group of large, lightly-stained cells situated *directly* beneath the apical initials (fig. 2). Because of their large size, irregular arrangement, huge nuclei, prominent and unevenly thickened walls, and relatively infrequent divisions, the central mother cells diverge strongly from the features usually associated with the primordial meristem in the seed plants. Of particular interest, however, is the renewed mitotic activity which appears at the lateral and basal margins of the zone of central mother cells, since from these areas there originate the bulk of the *peripheral tissue zone* and the *zone of rib meristem* (fig. 2b). The relation of this peculiar zonation to the differentiation process is interesting. As in many conifers, the *peripheral tissue zone* is composed of deeply-stained actively dividing cells and ultimately gives rise to the foliar organs, epidermis, cortex, and provascular tissue. But with reference to the origin of the pith, an important difference exists. In *Abies*, for example, this tissue is propagated directly by the progressive basipetal maturation of the cells of the central tissue zone (figs. 1, 1a). In *Ginkgo*, however, there is interpolated between the apical initials and the rib meristem from which the pith originates, a *central mother-cell zone,* distinctive in its structure and characterized by "random" cell expansion, rather than uniform cell division. From the standpoint of growth, this zone therefore may be regarded as a region of pronounced cell enlargement maintained between two well-defined areas of more active cell multiplication (figs. 2a, 2b, 2c).

Our knowledge of the cyto-histology of the shoot apex of cycads is at present unfortunately limited to the results of studies on three genera, so that caution must be exercised in making comparisons. Nevertheless, it does appear significant that a similarity exists between the zonal structure of the apex of *Ginkgo* on the one hand and the species of cycads examined, on the other. The resemblances seem particularly interesting in view of (1) the much greater size of the apex in the cycads, which may reach the enormous diameter of 3.5 mm. in *Cycas revoluta* Thunb., and (2) the striking differ-



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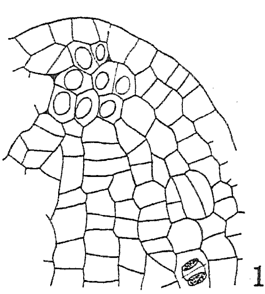

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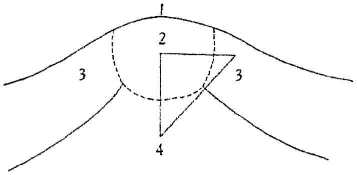

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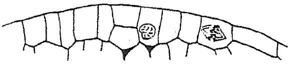

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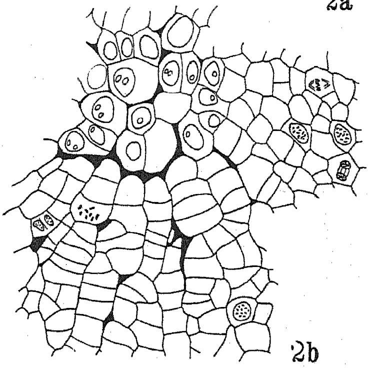

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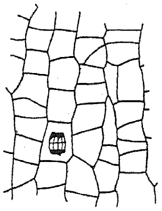

2c

FIG. 1. Outline of median longisection of the shoot apex of *Abies venusta* (diameter at base 230 microns) showing the position and extent of the apical initials (1), the subterminal "mother cells" (2), the zone of peripheral tissue (3) and the central-tissue zone or rib meristem (4). FIG. 1a, cellular structure of the sector of the apex indicated in figure 1. The small group of subterminal mother cells, shown with nuclei, is the common point of origin of rib meristem and peripheral tissue. Further explanation in the text. In this, and all subsequent drawings of cell detail, the magnification is approximately 250 diameters.

FIG. 2. Outline of median longisection of the apex of a long shoot of *Ginkgo biloba* (maximum diameter 321.75 microns) showing the position and relationships of the apical initials (1), the cup-shaped zone of central mother cells (2), the zone of peripheral tissue (3) and the rib meristem (4). FIG. 2a, the surface cells at the summit of the apex. Note prophase and recent periclinal division in the two apical initials shown in this section. FIG. 2b, cellular structure of the triangular sector of the apex indicated in figure 2. The zone of central mother cells is well-defined by the large size, irregular arrangement and shape, huge nuclei and uneven wall-thickenings of its component cells. The point of origin of the rib meristem and peripheral tissue from this zone (represented diagrammatically in figure 2 by the broken outline) is shown by a renewal in mitotic activity and a marked decrease in cell size. Note that certain of the original wall-thickenings of the central mother cells are "carried over" into the young rib meristem. FIG. 2c, small portion of rib meristem below that shown in figure 2b. Observe the filamentous cell-series and the absence of irregular wall-thickenings.

ences between the morphology of the shoot system of cycads and the maidenhair tree.

The zonal pattern of the shoot apex of *Dioon edule* Lindl.[2] is remarkably like that of *Ginkgo*. A deeply-situated and clearly delimited *central mother-cell zone*, derived from an extensive series of "initials," is the common point of origin for the massive zone of rib meristem and the bulk of the *peripheral tissue zone* (figs. 3, 3a). As in *Ginkgo*, these two zones can be traced to a renewed intensity in cell division at the edges and base of the zone of central mother cells (figs. 3b, 3c). Apparently a distinctive character of this zone, as contrasted with *Ginkgo*, is the greater variability in the size of the component cells. This probably reflects the wide degree of fluctuation in the relative frequency of cell division and cell enlargement in various portions of this zone. Johnson (1939) has recently examined the zonal structure of the apices of three Florida species of *Zamia*. It is evident from his drawings and descriptions as well as from observations made by the writer (1939a) that the histology of the apical meristem in these forms is closely similar in basic

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Explanation of figures 3 and 4

FIG. 3. Outline of median longisection of the shoot apex of *Dioon edule* (maximum diameter 1677 microns) showing the position and relationships of the extensive zone of initiation (1), the deeply-situated zone of central mother cells (2), the peripheral tissue zone (3) and the broad zone of rib meristem (4). Note the foliar primordia at the base of the dome-shaped apex. FIG. 3a, cellular structure of small sector through the initiation zone, showing a periclinally divided surface cell and the tiered arrangement of the inner cells. Note the irregular wall thickenings. FIG. 3b, cellular structure of the triangular sector of the apex indicated in figure 3. As in *Ginkgo* (fig. 2b) the addition of new cells to the zones of rib meristem and peripheral tissue occurs respectively at the base and sides of the zone of central mother cells (broken outline in figure 3). Note the wide variation in size and form of the central mother cells (shown with nuclei) and the massive wall-thickenings. These decrease markedly in prominence in the distal portions of zones 3 and 4. FIG. 3c, small portion of the rib meristem below the region shown in figure 3b. Prominent wall-thickenings are absent, as in the comparable region of the apex of *Ginkgo* (fig. 2c).

FIG. 4. Outline of median longisection of the very broad shoot apex of *Cycas revoluta* (maximum diameter 3412.5 microns) showing the four main tissue zones (zones 1–4). In contrast to *Ginkgo* and *Dioon*, there is no sharp demarcation between the central mother cells (2) and the adjacent zone of rib meristem (4). The broken outline however indicates that most of the peripheral tissue zone (3) originates from the edge of zone 2. The outer portion of the peripheral tissue, shown by the double outline on the flanks of the shoot apex, consists of the surface cells and their recent periclinal derivatives. FIG. 4a, cellular detail of small sector through the initiation zone (zone 1, fig. 4) showing frequency of periclinal divisions in the surface cells. FIG. 4b, a small group of central mother cells. Note large size of cells and prominent wall-thickenings. FIG. 4c, cellular structure of a small portion of the transition region between zones 2 and 3, showing the characteristic renewal in mitotic activity and the origin of the obliquely-arranged cell groups of the peripheral tissue. FIG. 4d, details of cell structure and arrangement at the point of origin of the rib meristem from the central mother cells (shown with nuclei).

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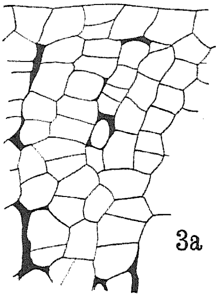
[2] A detailed account of the structure of the shoot apex of this cycad will be published in the near future.



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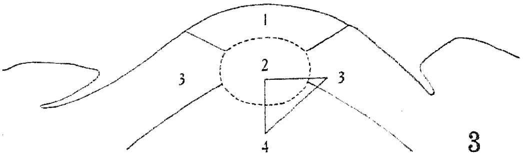

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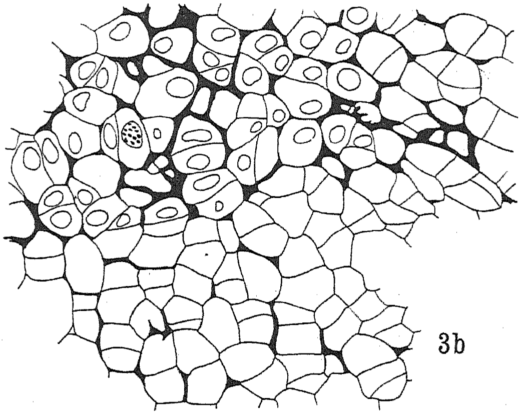

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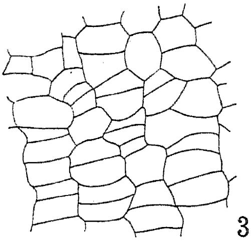

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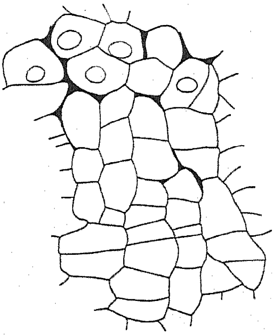
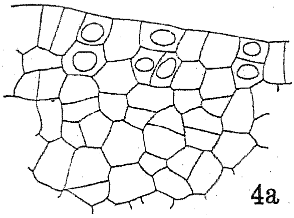


4d



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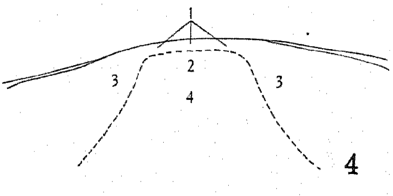

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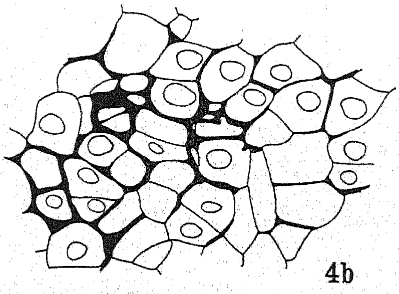
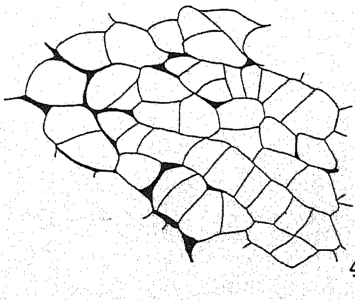


4b



4c

type to that of *Dioon edule*. The most intensive study, however, has been devoted to the shoot apex of *Cycas revoluta* (Foster 1939a, 1940). Whether one examines the relatively delicate conical apex of the seedling or the huge plateau or dome-shaped meristem of the adult plant, it is apparent that the *central mother cell zone* is less sharply demarcated than in either *Ginkgo, Dioon,* or *Zamia* (fig. 4). This is chiefly so because there exist no sharp boundaries between pith, rib meristem, and central mother cells (figs. 4b, 4d). In short, the renewal of mitotic activity in *Cycas* is most clearly seen at the edges of the central mother cells in connection with the propagation of the inner region of the zone of peripheral tissue (fig. 4c). All the species of cycads which have been investigated agree with *Ginkgo* in that the relatively enormous pith of the shoot axis originates from the rib meristem while the foliar organs, provascular tissue, epidermis, and cortex are produced by the zone of peripheral tissue. The latter, however, is not uniform in respect to the size or the staining qualities of its cells. Especially in *Cycas revoluta,* it consists of a shallow outer region made up of very small, deeply-stained cells and a more extensive inner region of larger and more obviously vacuolate cells (fig. 4).

ANGIOSPERMS

The fact is now well-established that in many angiosperms the cells of the shoot apex are arranged in two distinct zones, viz.: an outer zone or *tunica* composed of one or more layers of small, essentially similar, thin-walled cells enclosing an inner zone or *corpus* in which the cells are irregular in size and arrangement.[3] Under the influence of the tunica-corpus theory (Foster 1939b, Rüdiger 1939) the chief points for investigation have been (1) a determination of the number of layers composing the tunica and (2) the respective roles of tunica and corpus in the initiation of leaf and axillary-bud primordia. As a consequence, very little attention has been devoted to the cyto-histology of the shoot apex in flowering plants. It is clear, however, even with the meagre information at our disposal, that in addition to the more familiar type of shoot apex, there exist other types of zonal structure some of which invite direct comparison with the conditions just described for the more primitive gymnosperms. Furthermore, Gregoire (1938) has recently concluded that there is a fundamental difference between the zonal structure and growth of the terminal meristem of the flower and the vegetative shoot in the angiosperms (cf. Foster 1939b). Unfortunately, however, our knowledge of the comparative histology of vegetative and floral apices is at present meagre and final judgment of Gregoire's radical viewpoint must await the results of further research (cf. especially Brooks 1940 and McCoy 1940).

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[3] cf. postscript.

Cactaceae. Boke[4] has recently completed a study of the structure of the shoot apex in two species of this much-neglected family, viz.: *Opuntia cylindrica* DC. and *Trichocereus spachianus* Riccob. In both of these species, the surface cells of the apex form a more or less discrete layer or "tunica." The internal tissue of the apex, however, does not correspond in structure or behavior to the corpus region of such "typical" angiosperms as *Carya* (Foster 1935), *Rhododendron* (Foster 1937), or *Acacia* (Boke 1940). On the contrary, a zonal pattern obtains which recalls the situation in the apex of *Ginkgo* or *Dioon.* From the sides and base of the well-defined zone of vacuolated, irregularly arranged thick-walled cells there arise respectively the peripheral tissue zone and the zone of rib meristem. The latter differentiates into the pith and in *Trichocereus* also into the medullary vascular system while the peripheral tissue zone gives rise to the leaves, areoles, epidermis, cortex, and the main system of vascular bundles.

Palmaceae. Ball[5] has made a comparative study of the shoot apices of *Phoenix canariensis* Chaub., *Phoenix dactylifera* L., *Washingtonia filifera* Wats., and *Trachycarpus excelsa* Wendl., and the results of this investigation clearly indicate the existence of two distinct types of zonal structure. In *Washingtonia* and *Trachycarpus,* the tunica is biseriate and lies directly in contact with a poorly-defined corpus zone from which the rib meristem originates. The apex of *Phoenix,* however, exhibits a very divergent zonation. This consists in the presence of a large zone of small, lightly-stained, and irregularly-arranged cells from the sides and base of which, by means of cambial-like cell divisions, there arise respectively the peripheral and rib meristem zones. A further but less significant contrast is produced by the presence in *Phoenix* of a uniseriate tunica.

SUMMARY

A brief description and comparison have been given of the main results of recent studies on the cyto-histology of the shoot apex in certain gymnosperms and angiosperms. The most significant implications of these investigations may be summarized as follows:

1. The so-called primordial meristem of the shoot apex in seed plants cannot be regarded as either "simple" or "undifferentiated" in structure. On the contrary, the cells of this meristem are segregated into more or less well-defined *tissue zones* which are demarcated by such characters as cell size, the structure and intensity of staining of the protoplast, the relative thickness of the cell wall, and the proportional rates of cell division and cell enlargement.

2. The extent and relationship between the various tissue zones appear to reflect the type, direction, and distribution of growth in the apex. From

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[4] The results of this study will be published shortly.

[5] A detailed paper describing this investigation is in course of preparation.

this aspect, the various zonal patterns which have been described are of interest from a morphogenetic as well as a purely comparative standpoint. In the *peripheral tissue zone*, growth is manifested largely in cell division and there is a pronounced tendency to delay cell maturation. It seems significant therefore that this highly active zone is the area of initiation of foliar structures and provascular tissue in various groups of seed plants. The *zone of central mother cells*, which is so prominent in the apices of some plants, is a region characterized by impressive *cell enlargement* rather than "uniform" cell division (figs. 2b, 3b, 4b). The renewed mitotic activity which occurs at the sides and base of this zone is very suggestive of the accumulation of some type of hormone which stimulates or controls cell division. Finally, the *zone of rib meristem* which is composed of vertical, filamentous series of genetically-related cells, represents a tissue of the apex typified by polarized growth and progressive enlargement and cell maturation (figs. 1a, 2c, 3c, 4d).

3. In the light of the studies reviewed in this paper, it is very doubtful whether the importance usually attached to the "initial" cell or cells in a growing apex is justified. On theoretical grounds, it is admitted that in many gymnosperms all the tissue of the apex originates from the division of surface cells (figs. 1a, 2a, 3a, 4a). But whether these cells are constant in number, form, and sequence of division is highly doubtful. In the massive apex of *Cycas revoluta* for example, it is obvious that a very large number of morphologically identical surface cells and their recent derivatives collectively represent an *initiation zone*. However, no one cell or group of cells seems to dominate in this zone (fig. 4a). Comparable difficulties also arise with the more delicate apices of such angiosperms as *Acacia*. Here the zonal pattern consists of three more or less discrete tunica layers which envelop a central zone or *corpus*. According to Boke's (1940, p. 77) observations, however, "tunica and corpus are not rigidly defined" zones and furthermore it proves impossible to designate any particular series of superposed cells as the "initials" of the tunica layers. In view of these facts, it seems that the question of the number of initial cells is relatively insignificant as compared with the broader problem of the coordinated pattern of growth which expresses itself in the various types of zonal structure which have been described.

4. The picture of the apex which emerges from these studies is essentially dynamic in character. Indeed the evidence from comparative histology supports the recent conclusion of Thoday (1939) that "the shoot apex is a self-determining and dominant center of development."

5. From the standpoint of our present knowledge, there is no sure indication as to the nature of the most primitive type of apical meristem in the shoot of seed plants. The zonal pattern in the apices of *Ginkgo* and certain of the cycads may well represent an extremely ancient condition. But the

striking parallel in zonal structure furnished by certain angiosperms indicates the urgent need for a continued systematic exploration of the cyto-histology of the shoot apex of seed plants along broad comparative lines.

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Postscript. The tunica-corpus theory has received support from the recent experimental studies of Satina, Blakeslee and Avery (1940a) whose paper was published after the presentation of the present article. These investigators succeeded, by means of treating seeds with dilute solutions of colchicine, in inducing various kinds of periclinal chimeras in *Datura stramonium*. It was found that each of the two layers of the tunica, as well as the outermost "layer" of the corpus of the shoot apex responded *independently* to the colchicine treatment in that "any one of these germ layers in the chimeras may remain diploid, with cells containing 24 chromosomes, while the others become polyploid with tetraploid or octoploid cells." These variations in chromosome number and size of the cells are particularly useful from an histogenetic standpoint because they provide a way of determining accurately the role, in this plant, of tunica and corpus in the initiation of foliar and floral organs and in the differentiation of the primary tissues of the axis (cf. also Satina, Blakeslee and Avery, 1940b). In the writer's opinion, however, the attempt of these authors to apply Hanstein's (1868) terms "dermatogen," "periblem," and "plerome" in the description and interpretation of the structure of the shoot apex in *Datura* is likely to lead to confusion and, from a comparative viewpoint, is quite unjustified. As I have shown in a recent article (Foster 1939b), Hanstein's histogen theory has no general validity for the seed plants and hence its basic assumptions, while applicable to certain *individual* cases, do not assist in understanding the fundamental nature of organ and tissue differentiation at the shoot apex in the spermatophytes as a whole (cf. especially Schoute 1903, pp. 90–93, and Sharman 1940).

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THE PROLIFERATION OF DANDELIONS FROM ROOTS[1]

E. NAYLOR

(WITH SIXTEEN FIGURES)

Very few scientific investigations have been made on the propagation of dandelions from the roots, although many have observed that new plants appear after the tops have been removed. Munson (1903) says that the general practice of cutting "greens" causes more plants to appear. As many as 6 new crowns were observed on plants which had been decapitated. McCallum (1905) in a series of papers on regeneration in plants merely remarks that when roots of *Taraxacum* are cut into several pieces each piece formed new shoots. Longyear (1918) devotes a small portion of a paper on dandelions to propagation by root cuttings, and says that roots produce new plants at any place when cut. Pieces an inch long formed new plants after 18 days. He also observed that clusters of many new plants appeared after the tops had been removed from old plants growing in a lawn.

In the present study as many as 20 separate shoots have been isolated from the end of a single root cutting 1 cm. in diameter. A small ring of greenish callus develops near the center of the cut surface, and from this tissue the young leaves are differentiated in great profusion. Such remarkable capacity for vegetative reproduction from the roots explains the difficulty of eradicating this common plant.

METHODS

Cuttings were obtained from a small group of plants growing in an open lawn at the New York Botanical Garden. These plants have been identified as *Taraxacum laevigatum* (Willd.) DC.[2] The roots were washed and cut into transverse segments varying in length from 4 to 6 cm. After removal of the latex from the cut ends with cold water, the root pieces were placed upon moist filter paper in Petri dishes. Transverse and longitudinal sections were removed from the cut surfaces at daily intervals, fixed in medium chromo-acetic acid, dehydrated in ethyl alcohol, and embedded in paraffin. Sections were cut 8 microns in thickness and stained with Heidenhain's iron-alum haematoxylin or with Delafield's haematoxylin and safranin.

A maceration method described by Curtis (1940) was used to aid in the identification of the phloem elements. Small pieces of tissue were allowed to stand 24 hours in a mixture of one part of hydrochloric acid to four parts of 95 per cent ethyl alcohol, then washed in 10 per cent ammonia water. The separated cells were stained with an alcoholic solution of anilin blue.

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[1] This study was made at the New York Botanical Garden during a leave of absence granted by the University of Missouri.

[2] Specimens are deposited in the Herbarium of the New York Botanical Garden.

For the study of the primary root seedlings were grown on moist filter paper and in sand cultures. Seeds collected at various times during the summer and fall germinated within two or three days.

STRUCTURE OF THE ROOT

Several investigators have contributed to our knowledge of the internal structure of the dandelion root. De Bary (1884) described the fleshy root and concluded that it was composed of secondary phloem which consisted of parenchyma, sieve tubes, and articulated laticiferous vessels. Jeffrey (1917) remarked that the phloem was much better developed than the xylem, and contained certain dark concentric bands. These circular bands not only mark the position of the latex tissue, but that of the sieve tubes as well, which cannot be clearly distinguished from the former. Haberlandt (1914) described in some detail the articulated latex tubes of plants, and remarked that they were characteristic of the Cichoriaceae. Curtis (1940) has given the most complete description of the phloem tissues in the dandelion root. By the use of special macerating methods he was able to demonstrate the sieve tubes and latex elements arranged in concentric zones in the parenchyma. The findings here presented are in harmony with those of Curtis.

The primary root and the first leaf are well differentiated in a seedling 10 days old, as shown in figure 1.

A slight thickening immediately below the cotyledons is already evident; it is this region which continues to enlarge to form the fleshy root, as is demonstrated in figure 2.

Internally the primary root exhibits the usual arrangement of epidermis, cortex, and stele. The primary xylem is diarch (fig. 3). The phloem is largely parenchymatous, and the pericycle is often difficult to distinguish. The endodermis consists of a single row of cells with walls not much thicker than those of surrounding tissues. The cells of the cortical parenchyma are large and thin-walled, and some show signs of disintegration and the formation of air spaces. Granular materials present in some of the cortex cells give a protein reaction with nitric acid. Starch is not present in any portion of the root. The epidermis is variable in appearance. It may consist of a single layer of thick-walled cells, or it may have collapsed and partially disappeared so that the outer cells of the cortex form the surface of the root.

In a seedling four weeks old secondary development has started in the xylem and phloem regions, and other changes are evident within the cortex. Numerous scalariform vessels develop on either side of the primary xylem, and many parenchymatous phloem cells are rapidly differentiated. The cells of the endodermis undergo numerous divisions, new radial walls appearing at regular intervals (fig. 4). The pericycle divides both radially and tangentially and keeps pace with the endodermis in the rapid increase in diameter of the stelar region.

The fleshy root of a plant several months old consists almost entirely of secondary tissues. Two major regions can be identified in transverse sections; the relatively small central cylinder of xylem, and many concentric bands of secondary phloem which somewhat resemble annual rings. These concentric bands, which make up the bulk of the root, consist of rather narrow zones of sieve tube and latex cells which alternate regularly with similarly arranged broader zones of parenchymatous cells. The latter cells have thin walls, and occur in regular vertical and radial rows corresponding in arrangement to the cambium cells from which they originate (fig. 8). At fairly regular intervals the parenchyma interrupts the bands of sieve tube and latex cells, forming indistinct phloem rays. It was not found possible to determine the age of the root by counting the bands of secondary phloem.

The central cylinder of xylem is composed of secondary tracheids and tracheae and xylem parenchyma, as shown in figure 6. There is little evidence of ring formation in this region. A single cambium layer is found outside the last formed secondary xylem.

Laticiferous cells are abundant in the dandelion root, confined to the phloem region. These cells appear to originate from the cambium; they elongate rapidly and coalesce to form continuous tubes. The result is a complex net-like formation, very closely associated with the sieve tubes and embedded among the elongated cells of the parenchymatous phloem, as illustrated in figures 5 and 7. The sieve-tubes are long and narrow, not numerous, and have sieve openings only on the end walls. Both the latex and sieve tube cells are difficult to demonstrate in sections, but can easily be observed after macerating and staining.

There is no trace of the pericycle, endodermis, cortex, or epidermis in old fleshy roots. A phellogen layer is found near the periphery of the root, where it originates in the parenchyma cells of the secondary phloem. In young roots the phellogen appears first in the outer cortex, later in the pericycle. Secondary thickening takes place rapidly in the dandelion root and results in the addition of numerous bands of secondary phloem and a small amount of secondary xylem.

THE DEVELOPMENT OF NEW PLANTS

The root pieces selected for study were mostly from the middle of the fleshy root; they measured from 8 to 10 mm. in diameter. The callus appears on the second or third day in the form of a band lying immediately outside the xylem cylinder and completely surrounding it, as illustrated in figure 14. After five or six days the callus has developed a green color and has organized numerous leaf primordia, as shown in figure 15. The callus enlarges rapidly, and grows out over the cut surface so that one may sometimes make a false assumption about its origin. The young leaves differentiate quickly and their dentate margins are easily recognizable on the seventh or eighth day; they may reach a length of 2 cm. on the tenth day after the cutting is made (fig. 16).

The first internal evidence of new growth appears on the second day in the parenchymatous cells of the last formed two or three bands of secondary phloem near the xylem cylinder. The cells responsible for the new parts are considerably elongated, as shown in figure 8. Mitotic divisions occur at right angles to their long axes. Such activity may be found in the outermost cells of the cut surface, as in the cutting shown in figure 9, or may be confined to cells which are several cell-layers below the wounded surface. Rapid enlargement of these newly formed cells of the phloem parenchyma results in the external appearance of concentric rings of callus. Continued mitotic activity soon renders it impossible to distinguish the original parenchymatous cells; the result is a homogeneous mass of meristematic cells. The outer bands of secondary phloem near the periphery of the root are never active in proliferation.

Differentiation proceeds rapidly and by the third day small groups of cells containing densely staining protoplasm can be identified from one to several cells below the surface (fig. 10). These are the leaf primordia, which at this early stage of development have a distinct cellular pattern. Each consists of a central mass of cells in which divisions occur at various angles, and a single outer layer of cells in which anticlinal divisions predominate. Rapid cell divisions and elongation in the center of the mass cause the entire primordium to assume the shape of an inverted cone, as shown in figures 11 and 14. From these masses of cells the young leaves are differentiated in about 3 days. The details of the development of the leaf blade were not studied.

The development of vascular tissue begins at approximately the same time that the leaf primordia are initiated. Groups of meristematic cells situated deeper within the callus than the leaf primordia produce short vessel

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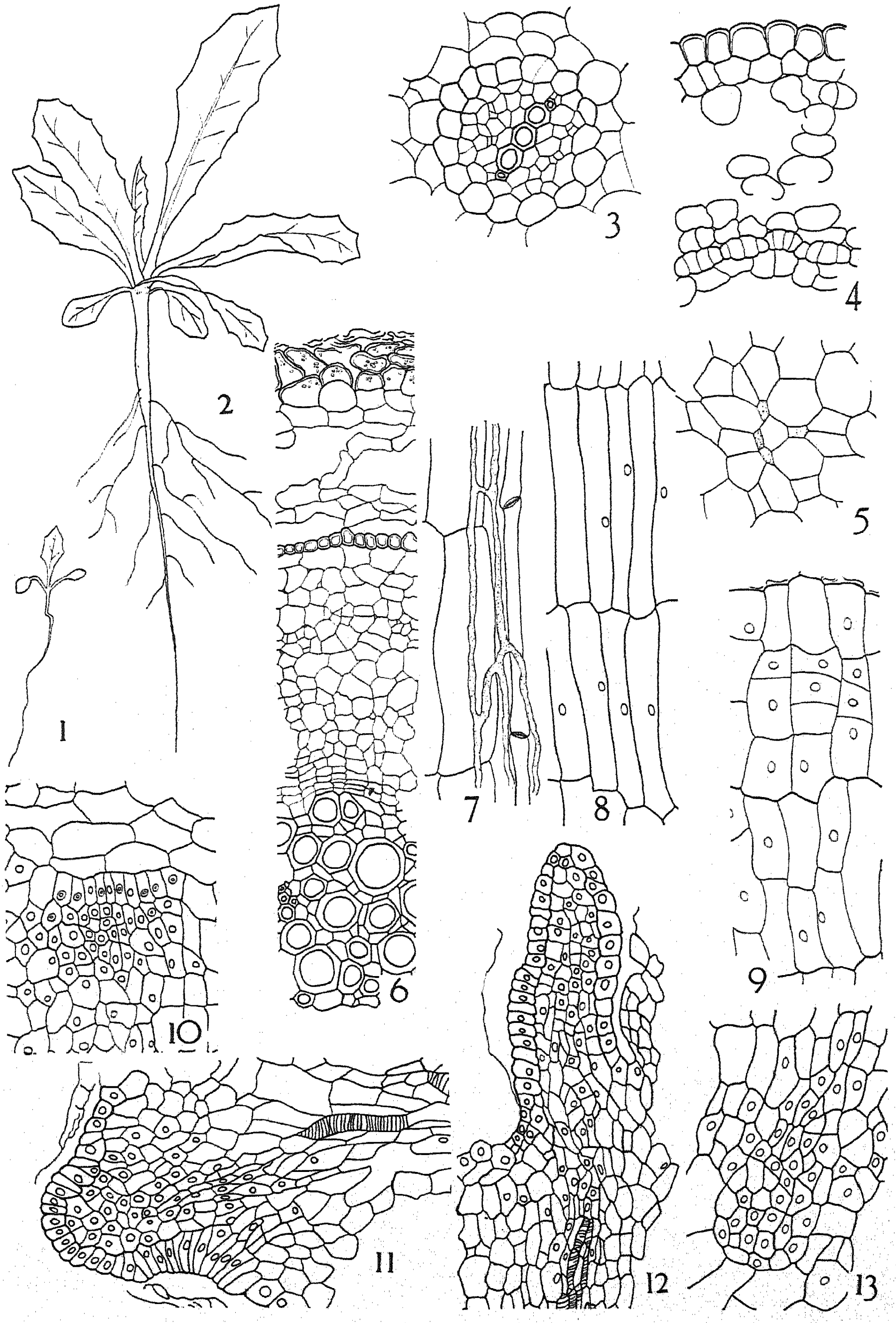
Explanation of figures 1–13

FIG. 1. Seedling 10 days old. × 0.4. FIG. 2. Seedling 4 weeks old. × 0.6. FIG. 3. Stelar region of very young root. × 190. FIG. 4. Cortex of young root showing radial divisions in cells of the endodermis, also formation of air spaces. × 190. FIG. 5. Sieve tube cell, latex cells (stippled), and surrounding parenchyma of the secondary phloem. × 200. FIG. 6. Cross section of young root after secondary thickening has begun. Epidermis replaced by outer cortex parenchyma, endodermis still evident, and stele making up major portion of the root. × 180. FIG. 7. Elongated sieve tube cell, branching latex cells, and phloem parenchyma. Preparation made after macerating and staining with anilin blue. × 200. FIG. 8. Phloem parenchyma cells, showing the regular arrangement. × 180. FIG. 9. Cell formation after two days in phloem parenchyma underneath the cut surface. × 200. FIG. 10. Formation of leaf primordium on fourth day. × 180. FIG. 11. Leaf primordium on fifth day beginning to break through surface layers. × 180. FIG. 12. Leaf primordium on seventh day; vascular system partly established. × 180. FIG. 13. Root formation from the distal end of the cutting after two weeks. × 180.



segments, which at first have no particular orientation toward the vascular system of the old root. The vessels are mostly of the scalariform or reticulate type; pitted forms were not found. Differentiation of such xylem elements takes place very rapidly, and the order of maturation is both forward toward the surface of the callus, and in the opposite direction toward the phloem parenchyma. This activity continues until the vascular connection is completed between the leaf primordium and the secondary xylem. The vascular cambium may also form additional xylem cells. Occasionally vascular tissues were found to develop within the callus before the formation of the leaf primordia. The degree of differentiation of new parts is not the same at any one time in the entire callus, as is illustrated in figures 14 and 15. Leaf formation may continue for several weeks.

New roots developed from the distal ends of the cuttings, and generally

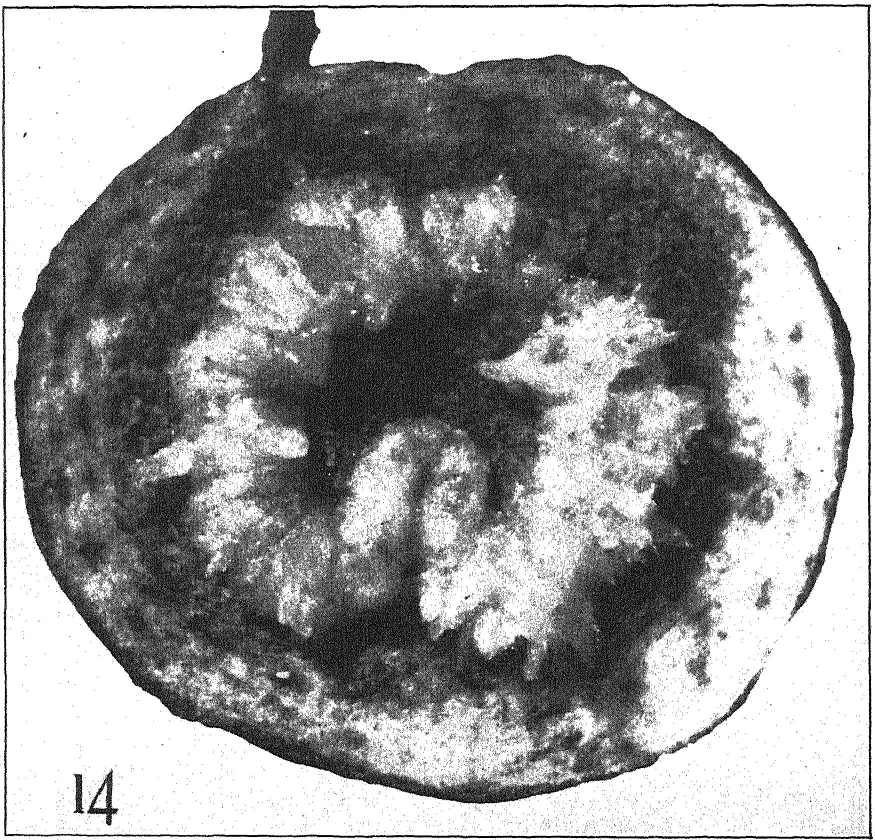


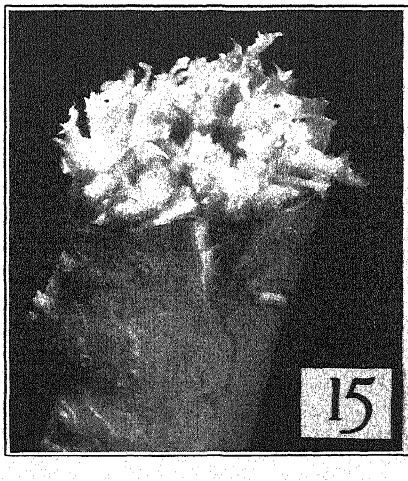
FIG. 14. End view of root, showing development of the ring of callus and leaf primordia after five days. (Photograph by courtesy of the New York Botanical Garden.)

did not appear until several days or even weeks after the shoots had formed at the proximal end. Their origin is very similar to that of the shoots. A band of callus is produced outside the xylem parenchyma, but its growth is not very vigorous, and it remains in a semi-dormant condition while shoot development takes place at the proximal end of the old root. The new roots emerge directly from the callus. A few lateral roots appeared near the stumps of old branch roots which had previously been removed.

Internally the callus at the distal end of the cutting, like that at the proximal end, originates from the phloem parenchyma. The root tips are formed from meristematic cells located a short distance below the surface (fig. 13). Vascular connections are established in a way similar to that described for the shoots. Roots have not been observed to develop with the shoots at the proximal end of root cuttings.

POLARITY

Leafy shoots were the only new parts found to develop at the proximal end of the cuttings used in this study. At the distal end a similar type of callus formation takes place, but only roots were produced. Attempts to change the polarity of the root by inverting pieces and allowing them to stand in a vertical position in the moist chamber were unsuccessful. Lateral roots appeared occasionally from the sides of the old roots. Goebel (1905) demonstrated shoot formation from the distal end of root cuttings of dandelion when the growth at the shoot pole was arrested by covering with wax or plaster. Wiesner (1892, p. 112) was also able to induce shoot formation



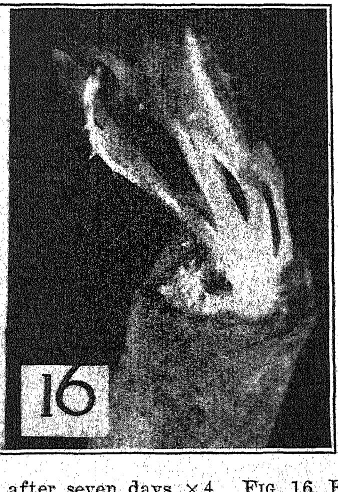


FIG. 15. Side view of root and young shoots after seven days. × 4. FIG. 16. End of cutting showing young shoots after ten days. × 2.5. (Photographs by courtesy of the New Botanical Garden.)

from both ends of root cuttings when they were kept in the dark. I have been unable to duplicate his results. Roots were grown both in the light and the dark, and the callus cut off repeatedly, but cuttings placed in the dark behaved like those placed in the light except for the failure to develop green color.

When fleshy roots were cut lengthwise along the median line both halves developed leafy shoots within 7 days. The new parts originated from phloem parenchyma and appeared in continuous strips on either side of the xylem cylinder.

Leaves of dandelion plants collected in April and May failed to develop any new parts when placed in moist sand in the greenhouse. They turned yellow and died within a period of two weeks. Stingl (1909) also failed to get regeneration from detached leaves.

SUMMARY

On root cuttings of dandelion in moist chambers proliferating tissue appears in two or three days.

The mature main root consists largely of phloem parenchyma, in which are embedded concentric rings of sieve tubes associated with laticiferous ducts.

The new parts originate from the parenchyma of the secondary phloem.

Shoots are formed at only the proximal end of the cuttings, and roots only at the distal end or occasionally along the sides.

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METABOLISM OF ASCORBIC ACID IN COWPEA PLANTS

MARY ELIZABETH REID

(WITH EIGHTEEN FIGURES[1])

A study of daily fluctuations in the ascorbic acid content of cowpea plants has been under way in this laboratory during the past four years. Announcement of the project was made previously (Reid 1939). Moldtmann (1939) reported a diurnal variation in the percentage content of ascorbic acid in leaves of *Fagus silvatica* and *Lamium album*. Increases occurred during the day and losses at night. Smith and Gillies (1940) found a maximum value in potato leaves in the early forenoon and minimum values toward the end of the night. Considerable fluctuations also occurred during the day. Kohman and Porter (1940) observed similar diurnal alternations in the tops of tomato plants. The results in these latter studies were presented also on a percentage basis. Reid (1940) reported briefly on fluctuations in the total quantity of ascorbic acid in leaves, stems and roots of young cowpea plants. The diurnal changes in ascorbic acid values were also determined on a percentage basis.

The first experiment herein described was conducted to determine the effect of the normal daily light and dark periods of July and early August upon the accumulation of ascorbic acid and growth of young cowpea plants. The effect of twenty-four-hour dark-periods immediately preceding the ascorbic acid assays was studied in the second experiment. A study was also made of the ability of cotyledons and of different-sized particles obtained from broken cotyledons to synthesize ascorbic acid when subjected to conditions favorable to germination.

PROCEDURE

Cowpea seedlings were grown in washed white sand, some with and some without a mineral nutrient solution. Ascorbic acid determinations by the indophenol method[2] were made daily on each of the two types of cultures. In the first experiment plants were washed free of sand at 4:15 a.m., the end of the dark period and others at 7:00 p.m., the end of the light period. The leaves, roots, stems, and cotyledons were weighed and analyzed separately. In most of the tests ten plants were assayed. In the second experiment plants were prepared for the tests each day at 1:00 p.m., at which time one culture with and one without added nutrients were analyzed. Similar cultures were placed in a dark chamber and assayed for ascorbic acid twenty-four hours later. This procedure was repeated each day throughout the experimental period.

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[1] Figures 12–18 are published at the expense of the author.

[2] The validity of the results obtained in these tests depends upon the supposition that the reducing action of the plant tissue extracts is to be attributed entirely to ascorbic acid. The titrations were made rapidly and the readings were taken when the end-point color was maintained for approximately 20 seconds. Considering the speed of the reaction and the relatively low pH of the extracts, there is no obvious reason for assuming that other substances were involved in the reaction.

OBSERVATIONS

The ascorbic acid content and the green weight of young plants which received mineral nutrients are shown in figure 1 and those of plants grown without added nutrients in figure 2. In both series the ascorbic acid increased in the plants during the dark periods as long as the stored food reserves in the cotyledons lasted, which was until the fifth day. After this time no gains were found during the dark period. On the contrary, there were losses after the fifth day in plants which received mineral nutrients and after the sixth day in those grown without added nutrients. Losses of as much as 17 per cent of the total ascorbic acid were found in the plants receiving mineral nutrients and of 8 per cent in those without added nutrients. Since there is greater steepness of the curve representing the ascorbic acid content of the fertilized plants and also since more disappeared at night, these plants must have synthesized considerably more of the vitamin than the unfertilized plants. The green weights of the former were also greater. In both groups the green weights tended to increase at about the same rate in the dark periods as in the light. The above results with entire plants were attained by separate analyses of leaves, stems, and roots. The data for the individual organs were as follows:

The leaves of plants receiving mineral nutrients gained in ascorbic acid during the third and fourth nights but from the fifth night until the termination of the experiment, losses, increasing with each succeeding night, were found. The rate of growth of the leaves in the light and dark periods tended to be equal (fig. 3). The results with plants grown without added nutrients were similar, although values for both growth and ascorbic acid were lower. Losses in ascorbic acid were also found during the fifth night

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Explanation of figures 1–6

The green weight and ascorbic acid values at successive stages of development shown in figures 1–9 were determined at the end of each daily light and dark period. The broken portions of the lines represent the light periods and the solid segments the dark periods. Except where the contrary is specially designated, the graphs shown represent the average values in a plant grown with added nutrients.

FIG. 1. Green weight and total ascorbic acid values of entire plant. FIG. 2. Green weight and total ascorbic acid values of entire plant grown without added nutrients. FIG. 3. Green weight and ascorbic acid values of primary leaves. FIG. 4. Green weight and ascorbic acid values of roots. FIG. 5. Green weight and ascorbic acid values of stem. FIG. 6. Total ascorbic acid values expressed on a uniform scale for all organs of a plant.

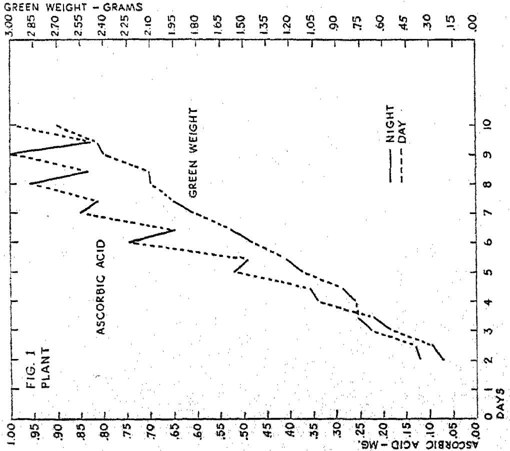
FIG. 1 PLANT

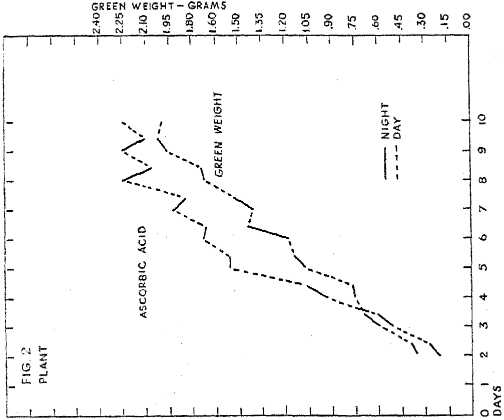
FIG. 2 PLANT

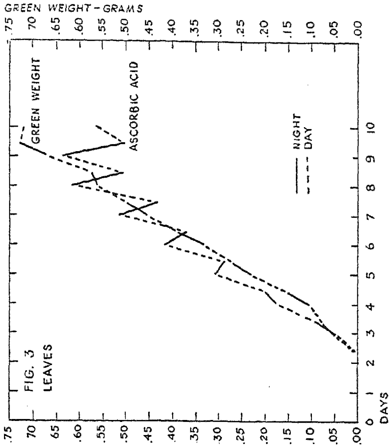
FIG. 3 LEAVES

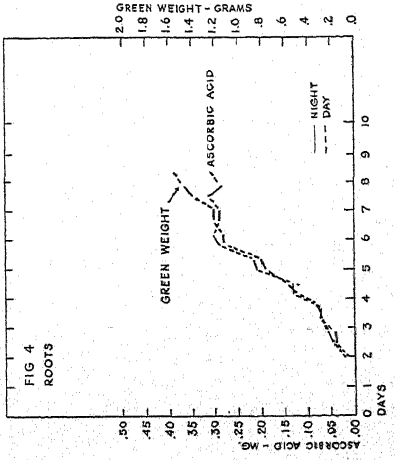
FIG 4 ROOTS

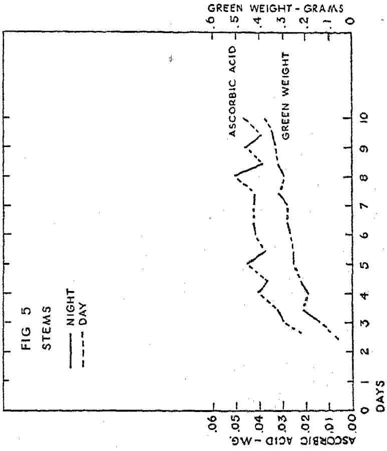
FIG 5 STEMS

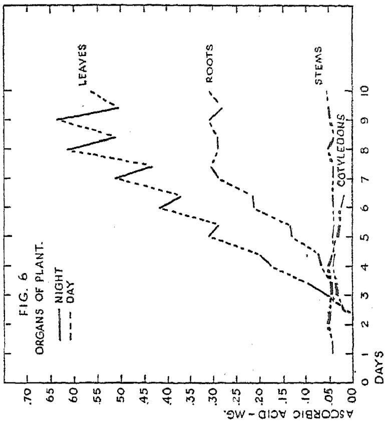
FIG. 6 ORGANS OF PLANT.

and on each night thereafter. The lag in rate of ascorbic acid accumulation and in increase in green weight between the ninth and tenth days occurred when the seedling leaves were fully developed.

Figure 4 shows the green weight and ascorbic acid values of the roots of the plants which received mineral nutrients. A fairly close relation is to be observed between the green weight and ascorbic acid content of the roots at successive stages of development up to the ninth day. A divergence between the values as the roots became older was also found in the plants grown without added nutrients. The green weights and ascorbic acid tended not to increase appreciably during the dark periods. In the plants grown without added nutrients and which consequently (Kraus and Kraybill 1918) had accumulated a much larger supply of mobilizable carbohydrates, there was a tendency for increases in both weight and ascorbic acid during the dark periods. Previous studies have shown a similar relation between available carbohydrate supply and growth of roots of tomato cuttings kept in darkness (Reid 1926). Decreases in ascorbic acid in roots did not occur with regularity during the dark period in any of the tests. It is possible, however, that translocation of the vitamin to the roots occurs in darkness or that some synthesis occurs within the root with the result that losses and gains are approximately balanced.

The ascorbic acid and green weight values of stems of plants which received mineral nutrients are shown in figure 5. No gains in ascorbic acid during the dark period were noted after the food reserves in the cotyledons were exhausted. Increases in green weight tended to be continuous and of about the same magnitude in the light and dark periods after the fourth day. The irregularity in the curve on the seventh day may be caused by slight variations in intensity of illumination of different cultures at the time of active growth of the hypocotyls. The light- and dark-period ascorbic acid values of all organs of the plant receiving added nutrients are shown on a uniform scale in figure 6. The leaves contained about 65 per cent of the total quantity of the vitamin and the roots about 30 per cent in the eight- to ten-day stage of development. As the plants became older the proportion in the leaves became relatively greater and that in the roots correspondingly less.

The great difference resulting from expression of the metabolism of ascorbic acid as total amount or as milligrams per gram may be noted by comparing figures 1, 7, and 8. Figure 7 shows the ascorbic acid values of the entire plant and of the top only expressed as milligrams per gram and figure 8 the total ascorbic acid and green weight of the top excluding the cotyledons. The much smaller size of the diurnal fluctuations in the entire plant, as compared to those in the tops only, result from the fact that the roots, which constitute a relatively large proportion of the green weight of the entire plant, did not show fluctuations with regularity. Figure 9 shows the ascorbic acid content of the primary leaves on a percentage basis. The slope of the curve is strikingly different from that representing the progressive changes in total content (fig. 3). There was a marked gain in concentration and in total quantity of the vitamin on the third day when the chloroplast-containing mesophyll tissue was developing rapidly. Rapid growth on the fourth night resulted in a marked decrease in ascorbic acid on a percentage basis. The total values show that actually a considerable gain occurred during this time. During the light period on the fourth day only a very slight gain on a percentage basis was found whereas the total quantity in the leaves increased markedly. On the fifth night a very large loss of the vitamin on a percentage basis, undoubtedly caused chiefly by a rapid increase in the water content, and a very slight loss on a total basis occurred. During the light period on the fifth day and on each succeeding day there was a considerable increase on a percentage basis. Greater losses at night than gains during the day in vitamin concentration cause the downward trend of the percentage curve and smaller losses at night than gains during the day are responsible for the upward trend of the curve representing the absolute amounts of ascorbic acid. In plants having many full-grown leaves the influence of growth of a few young leaves during the night on the vitamin C percentage value of the entire mass of leaves would be comparatively slight. There would, however, tend to be an appreciable error as a consequence of the gain in water content which is known to take place at night even in fully grown leaves under the general atmospheric conditions of summer. For example, Lloyd (1913) found from 7 to 15 per cent higher water content at sunrise than in the afternoon in the leaves of cotton plants at Auburn, Alabama, and Tucson, Arizona; Miller (1917) reported a 5.4 per cent higher average water content in corn and 5.9 per cent higher value in kafir between 1:00 and 5:00 a.m. than between 1:00 and 3:00 p.m.

In view of these considerations it seems obvious that only by measurements of the absolute amounts of ascorbic acid either in the entire plant or in individual organs can the magnitude of diurnal changes in its content be shown with a fair degree of accuracy. When plants are considered in terms of their nutritive value with respect to vitamin C, expression of their ascorbic acid value on a percentage basis is both valid and practical but in terms of the performance of the plant itself it is not of any considerable value except when accompanied by an evaluation of the vitamin in terms of absolute amounts.

Figures 10 and 11 show the results obtained in the second experiment in which plants kept in darkness for twenty-four hours previous to testing are contrasted to those subjected to the normal day and night periods.

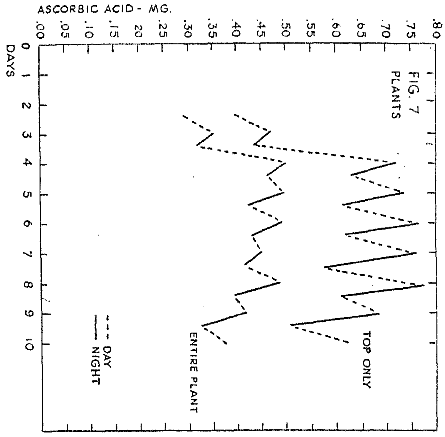

FIG. 7
PLANTS

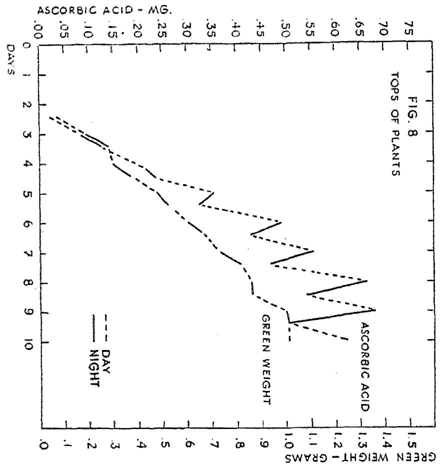

FIG. 8
TOPS OF PLANTS

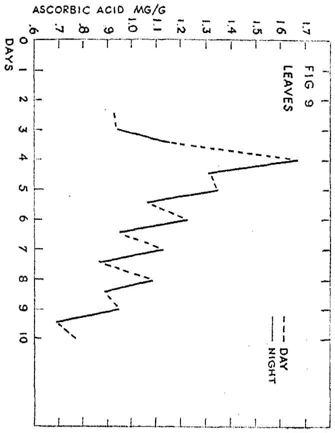

FIG 9
LEAVES

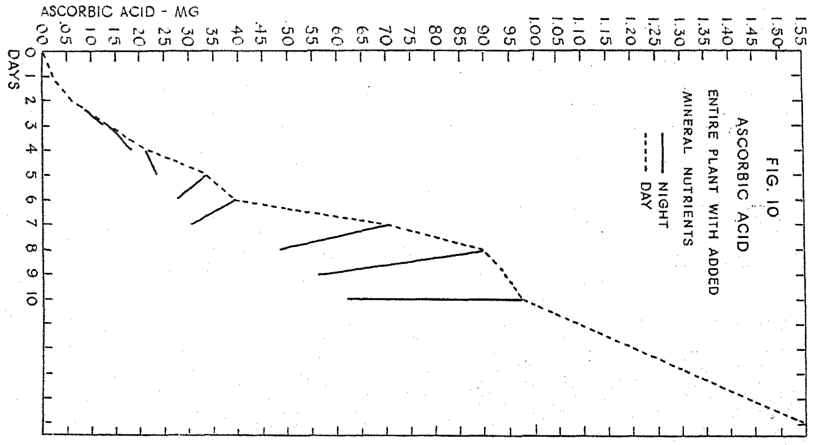

FIG. 10
ASCORBIC ACID
ENTIRE PLANT WITH ADDED
MINERAL NUTRIENTS

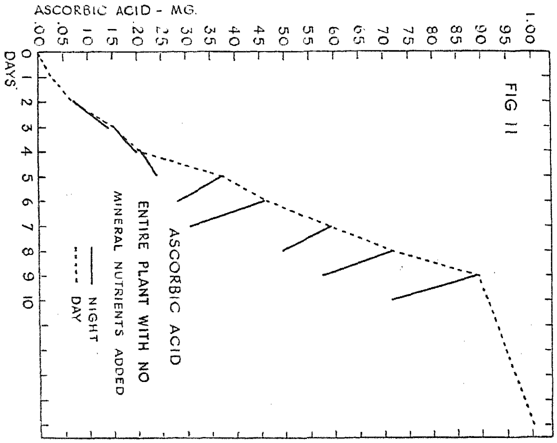

FIG 11

ASCORBIC ACID
ENTIRE PLANT WITH NO
MINERAL NUTRIENTS ADDED

The broken line shows the ascorbic acid content of plants subjected to the normal daily periods of daylight and darkness. The points at the free ends of the solid lines show the ascorbic acid content of the plants kept in darkness for twenty-four hours. The points are connected by the solid lines with the points representing the approximate content of the plants at the time they were placed in the dark chamber. Hence a slope upward of these lines represents a gain in ascorbic acid during the dark period and a slope downward represents a loss. It may be noted (fig. 10) that as in the previous experiment an increase in the total quantity per plant occurred each day until the stored reserves in the cotyledons were exhausted. After this time there were losses during the dark period. The plants grown without added nutrients yielded similar results, although growth was less rapid and losses of ascorbic acid during the dark period were smaller (fig. 11). A lowering of the vitamin C content by as much as 28 per cent in the plants which received nutrients and of 20 per cent in those not so supplied was found. These latter plants contained considerable starch at the end of the dark period. Hence, if plants form ascorbic acid from stored carbohydrates, it appeared that those employed in these tests lacked the capacity, at least to a measurable extent, to utilize their stored carbohydrates in the synthesis of the vitamin during periods of darkness.

The green weights of leaves, stems, and roots all increased during the dark period (figs. 12, 14, 16) and the gains were coincident with losses in the total quantity of ascorbic acid in the plant. Analyses of the vitamin C content of the individual organs revealed that the greater portion of the total loss during the twenty-four-hour dark period occurred in the leaves (fig. 13). However, in proportion to the total quantity present, the losses in the stems were of equal magnitude (fig. 15). The roots tended to show neither definite gains nor losses of ascorbic acid after the plants became independent (fig. 17).

Attempts were made to determine if all or part of the loss of ascorbic acid during periods of darkness may result from conversion of the vitamin to

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Explanation of figures 7–11

FIG. 7. Milligrams per gram fresh weight of ascorbic acid in entire plant and of top only. FIG. 8. Total ascorbic acid and green weight of top. FIG. 9. Milligrams per gram fresh weight of ascorbic acid in leaves.

In figures 10–17 the broken lines connect points representing ascorbic acid or green weight values of plants grown under normal daily alternations of light and darkness; the points at the free ends of the solid lines represent the values obtained with plants kept in darkness twenty-four hours previous to testing. Each point is connected by the solid lines with the point representing the approximate value of the culture at the time it was placed in the dark chamber. Except where the contrary is specially indicated, the graphs represent the average values in a plant grown with added nutrients.

FIG. 10. Ascorbic acid values in entire plant. FIG. 11. Ascorbic acid values in entire plant grown without added nutrients.

the dehydro form (Bessey 1938). Since the results were not conclusive the problem will be given further study. Moldtmann (1939) found no accumulation of dehydroascorbic acid following periods of darkness in the plants which he studied.

Tests have also been made to determine the course of ascorbic acid accumulation in cowpea seeds during the first twenty-four-hour period of germination. Seeds were supplied with moisture and kept at a temperature of 29° C. Ascorbic acid assays were made at two-hour intervals. Figure 18 shows the results. An indophenol-reducing action of the extracts was observed after a period of four hours and a considerable increase in the magnitude of the reaction was observed by the tenth hour. It is of interest to note that this followed the attainment of maximum absorption of water by imbibition. The increase in green weight after the fourteenth hour is doubtlessly a consequence of growth. At the end of the twenty-four-hour period the sprouts were about 1 centimeter long.

It was observed in other experiments that detached cotyledons placed on moist filter paper in Petri dishes and incubated for 20 hours at 29° C. produced almost as much ascorbic acid as intact seeds incubated similarly. The cotyledons of old seeds which had lost viability produced no ascorbic acid when placed under conditions favorable to germination. When a fine powder produced by grinding a weighed quantity of the cotyledons was incubated there was no rapid indophenol-reducing activity such as is characteristic of ascorbic acid. There was, however, a very slight but slow reaction with a fading end-point. These latter results were not in agreement with observations reported by Pereverzev (1937) who found that crushed cotyledons of legumes retained the ability to form vitamin C. Further tests with cowpea cotyledons were conducted to determine the reason for the discrepancy between the present and Pereverzev's results. Cotyledons cut with a scalpel so as to form a mixture of fine and coarse particles, when incubated under conditions favorable to germination, were found to have an ascorbic acid content almost equal to that of entire cotyledons. These results suggested that the size of particles into which the cotyledons were broken might be an important factor in causing the differences in the above mentioned tests.

A series of tests was conducted with cotyledons crushed and sorted into different sized particles. In each of the tests three grams of the material were placed on a double layer of filter paper in a Petri dish, and 5 cubic centimeters of distilled water added. The cover of the dish was raised slightly by

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Explanation of figures 12–18

FIG. 12. Green weight of leaves. FIG. 13. Ascorbic acid content of leaves. FIG. 14. Green weight of stems. FIG. 15. Ascorbic acid content of stems. FIG. 16. Green weight of roots. FIG. 17. Ascorbic acid content of roots. FIG. 18. Green weight and ascorbic acid content of seeds placed in germinators kept at 29° C. and tested at two-hour intervals during the first twenty-four hours.

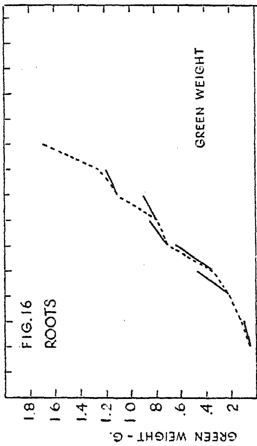

FIG. 16 ROOTS

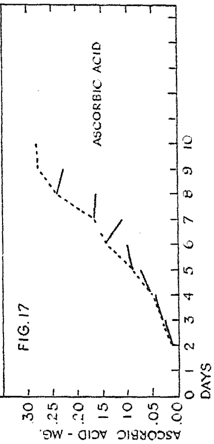

FIG. 17

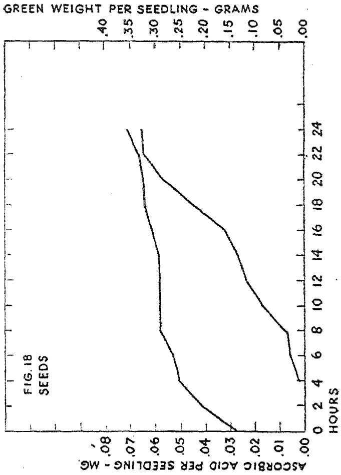

FIG. 18 SEEDS

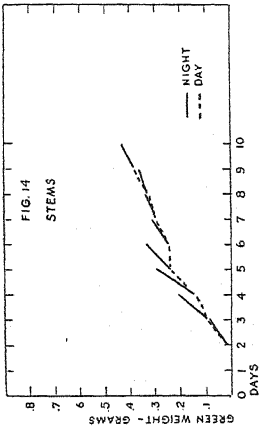

FIG. 14 STEMS

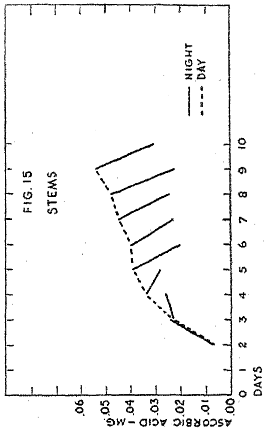

FIG. 15 STEMS

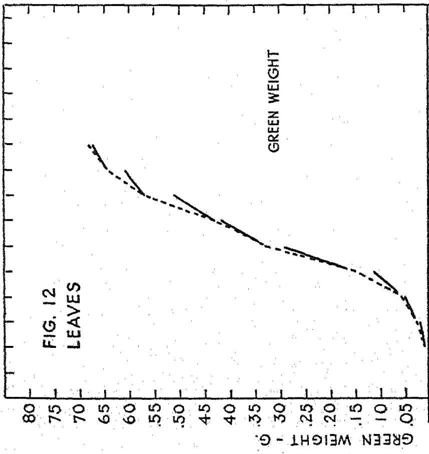

FIG. 12 LEAVES

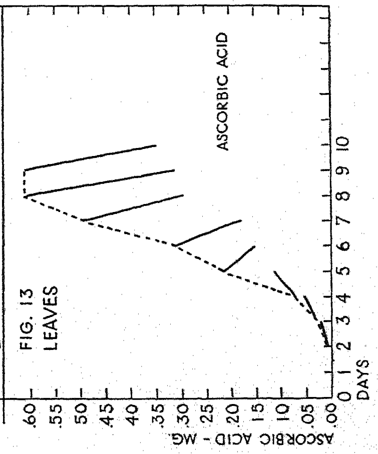

FIG. 13 LEAVES

a wedge of folded paper to provide for aeration. After incubating the culture at 29° C. for 15 hours, ascorbic acid assays were made. From the data presented in table 1 it appears that size of the cotyledon particles is a factor influencing the capacity for ascorbic acid synthesis.

TABLE 1

Effect of comminution of cotyledons into different sized particles upon their ability to synthesize ascorbic acid when exposed to conditions suitable for germination

Screen	Size of opening	Total ascorbic acid	Ascorbic acid
	mm.	*mg.*	*mg./100 g.*
Entire cotyledons	....	0.269	8.94
¼ normal size	....	0.246	8.20
10[a]	2.00	0.267	6.85
20	0.84	0.196	5.10
40	0.42	0.048	1.60
60	0.25	0.016	0.54
80	0.177	0.008	0.27
Over 80	....	Possibly a trace	....

[a] The data for each screen represent the values obtained with particles retained by that mesh but which passed through the openings of the preceding screens.

The results of these different experiments with cotyledons show (1) that the vitamin can be generated from a precursor stored within the cotyledons and that an influence from the plumule or radicle is unnecessary, and they suggest, furthermore, that vital processes are probably involved since the synthesizing capacity is lost when the tissues are finely pulverized, and also when viability is lost by aging.

DISCUSSION

After the plants used in these tests had exhausted the reserves in the cotyledons they lacked the capacity during the night to synthesize as much ascorbic acid as was being used, with a resultant loss. In fact, they may not have synthesized any, or the decrease may have represented the excess of loss over gain. The results show conclusively that ascorbic acid is metabolized in darkness. Similar metabolic processes probably occur also in light but they cannot be detected readily because of rapid synthesis in light. The fraction assayed constitutes supposedly the unusued portion only. Hence accumulation is measurable by present techniques but not the full magnitude of synthesis. The fate of the disappearing portion is not known with certainty. It may be destroyed in respiration or it may be used in some special type of synthesis. Experiments with plants kept at different temperatures have shown that it is lost during dark periods only when the temperature is high enough to permit growth, and that the more rapid the growth the greater the loss.[1]

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[1] These results will be described in another publication dealing with the effects of temperature on ascorbic acid accumulation in cowpea plants.

The failure of the plants employed in these experiments to increase their ascorbic acid in darkness following exhaustion of the reserves stored in the cotyledons suggests that the capacity to convert carbohydrates to ascorbic acid in darkness is very weak or may be entirely lacking. The ability to accumulate the vitamin in darkness during the period of utilization of the reserves in the cotyledons may be explained (1) by the storage during development of the seed of a closely related precursor which may be mobilized and reconstituted during germination or (2) by a somewhat different type of enzymatic action in the young seedling which may permit the conversion of stored carbohydrates such as starch to ascorbic acid. This capacity may be lacking or at least is relatively weak in the actively growing plant after it becomes independent of the cotyledonary reserves.

There is insufficient evidence to furnish a conclusive answer as to which, if either, of these hypotheses is correct, but there are, however, certain arguments in favor of a synthesis of a closely allied precursor. The relatively prompt reappearance of the vitamin when moisture is supplied also suggests a conversion from a closely related form. Previous study has shown that ascorbic acid accumulates in growing cowpea seeds approximately as long as the green weight continues to increase (Reid 1937). More recent investigations (unpublished data) have shown a similar relation in developing soybeans. Parsons (1920) pointed out that the vitamin might possibly pass into an inactive state on aging or drying and that it might be reconstituted in such physiological processes as the sprouting of seeds. Little attention has been given to this suggestion, however, since up to the present time there has been no obvious reason for questioning the ability of the plant to convert some of the mobilizable carbohydrates into ascorbic acid. Moreover, there has been considerable experimental evidence to support the viewpoint of a fairly direct conversion. Plants kept in darkness have been shown to increase their indophenol-reducing activity when supplied with sugar solutions of several types (Ray 1933, Reid 1938, Moldtmann 1939, Rubin *et al.* 1939, and others). There is no assurance in the reported tests, however, that the cultures were kept in a sterile condition. It is possible that micro-organisms may have produced indophenol-reducing substances other than ascorbic acid. Antiscorbutic tests of the product responsible for the increasing reducing activity in plants under the conditions described have not been reported. It is evident that further study is required before conclusions may be drawn on the ability of plants to convert carbohydrates into ascorbic acid. It is possible that they may be of use in such a synthesis but that the process is not so direct as has been postulated.

SUMMARY

Ability to increase the total ascorbic acid, as determined by reduction of

indophenol, during periods of darkness continues as long as the stored reserves in the cotyledons remain available.

After this time the plant lacks the capacity to use carbohydrates in the synthesis of the vitamin, or, if the conversion occurs, the rate is so slow that the metabolic loss masks the synthesis.

The loss is accompanied by growth. This suggests that the ascorbic acid may be destroyed in respiration or may be used in some special type of synthesis.

The possibility is discussed that the net loss or gain may not represent the magnitude of ascorbic acid synthesis or loss.

Evidence is presented which shows that the net magnitude of the diurnal fluctuations in ascorbic acid can be shown only by measurements of absolute amounts in individual organs or in the entire plant.

It is suggested that the synthesis of ascorbic acid during the dependent phase of growth is effected by the reconstitution of a closely related precursor stored in the seed during its development.

An influence of the plumule or radicle is unnecessary to effect synthesis of ascorbic acid in the cotyledons. The ability of crushed cotyledons to synthesize the vitamin appears to be dependent upon size of the particles.

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CALCIUM AND PHOSPHORUS AS THEY INFLUENCE MANGANESE IN FORAGE CROPS[1]

WM. A. ALBRECHT AND N. C. SMITH[2]

(WITH FIVE FIGURES)

Plant physiology has regularly recognized the significance of the degree of acidity of the soil, but has not yet clearly interpreted its significance in plant nutrition. Emphasis on lime additions to the soil for its modification of the degree of soil acidity has overshadowed attention to calcium as a nutrient, and/or as it serves in bringing other nutrients into the plant. Because the degree of hydrogen-ion saturation of the colloidal fraction of the soil is mainly the reciprocal of the loss therefrom of calcium ions, we have been inclined, in cases of crop failure, to attribute causal significance to the wrong one of these reciprocal factors. Studies of the significance of calcium in nitrogen fixation and plant nutrition were undertaken to determine more accurately the role of calcium in crop growth. The separation of its role in changing soil reaction from that in serving as plant nutrient, and in mobilizing other nutrients into the crop, served as a challenge. Its relation in this last respect to manganese in particular, one of the micronutrient elements, was chosen for study.

The importance of manganese in the nutrition of plants (5, 12, 13, 16) and of animals (9, 15, 18) has been established well enough to warrant attention to it in soil fertility. Its disturbed delivery to plants by soils near the neutral or alkaline reactions has been recognized (8, 11, 17). Such irregularities put the common practice of liming a soil for the sake of neutrality into the danger zone of general manganese shortage for plants in our extensive agricultural soils. Since calcium as a nutrient item, particularly for nitrogen fixation by legumes, has been separated from its effects in modifying soil acidity (1, 2, 3), the following study attempted to determine manganese movement into the crop when calcium modified the soil reaction as contrasted to that when calcium served as a nutrient without changing the reaction of the entire soil body in root contact. Phosphates were tested similarly as to their influence on the manganese.

PLAN OF STUDY

The soil used was the surface layer of a well weathered prairie soil of the Kansan glaciation, one of the planosols,[3] known as the Putnam silt loam. It is of acid reaction, pH 5.5, relatively low in organic matter and phosphorus, and developed to the point of having a marked clay concentration in the upper subsoil. Its exchange capacity is approximately 20 M.E. per 100 gms. of soil. This is usually saturated to about 50 per cent with hydrogen. The more common legumes will produce only poor yields on this soil.

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[1] Contribution from the Department of Soils, Missouri Agricultural Experiment Station, Columbia, Mo., Journal Series No. 686.

Acknowledgment is gladly made to Dr. Victor Ells for the spectrographic analysis; and to help by the National Youth Administration in growing the plants.

[2] Professor and Instructor in Soils, respectively, College of Agriculture, University of Missouri.

Amounts of treatments applied. Pot cultures were grown in quintuplicates of two legumes, sweet clover (*Melilotus alba*) and lespedeza (*Lespedeza stipulacea*), and of two non-legumes, bluegrass (*Poa pratensis*) and redtop (*Agrostis alba*). The soil treatments consisted of separate additions of calcium carbonate, of calcium phosphate and of sodium phosphate, and of joint additions of the calcium carbonate and calcium phosphate. The amounts of calcium carbonate applied to the soil were such as (a) would exchange slightly more than one-half of the replaceable hydrogen in one-fourth of the soil; and (b) would more than replace the total exchangeable hydrogen in this smaller soil portion. The phosphates were used in amounts that represented (a) liberal applications in practice, and (b) twice this amount.

Placement of treatments. The applications of calcium carbonate were made by distributing it (a) throughout all the soil in the pot, and (b) into the surface one-fourth of the soil. The calcium phosphate was applied similarly. The sodium phosphate was put into only the surface or one-fourth. The joint applications of calcium carbonate and calcium phosphate were used in the four possible combinations as amounts, and were placed into the surface or one-fourth of the soil only.

These placements of the calcium carbonate provided, in the first place, two different, but low, degrees of calcium saturation or of partial neutralization of the entire soil volume available to the plant. In the second place, they provided soils in which the surface areas alone had two different degrees of calcium saturation, namely one with more than 75 per cent and one in excess of complete calcium saturation, while three-fourths of the soil volume remained untreated. For simplicity's sake, these distributions of the additions to the soil may be spoken of by numbers as follows:

Treatment No. 1—Small amount throughout the entire soil volume.
Treatment No. 2—Large amount throughout the entire soil volume.
Treatment No. 3—Small amount through one-fourth or surface of the soil.
Treatment No. 4—Large amount through one-fourth or surface of the soil.

The phosphate additions represented different and higher degrees of saturation by the phosphate in the surface portion of the soil, and two different, but much lower, degrees of saturation when applied throughout the entire soil body. The combinations of calcium carbonate and calcium phosphate were used in the surface portion only, and represented the higher degrees of surface soil saturation by each of them. No manganese was applied.

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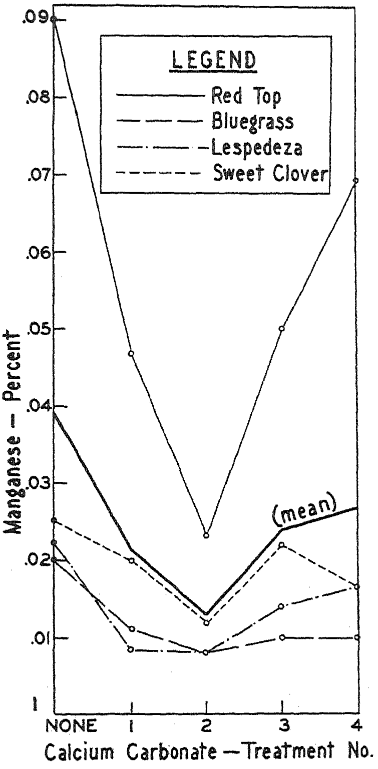
[3] According to *Soils and Men*, U.S.D.A. Yearbook of Agriculture, 1938.

Analytical methods. The crops were harvested at intervals of significant top growth so as to simulate grazing. Weight records of the harvests were taken. The crops were submitted to analysis by the standard gravimetric methods for the calcium and phosphorus and to the Lundegardh spectrographic method for manganese, and account was taken of the concentrations and totals in the crops.

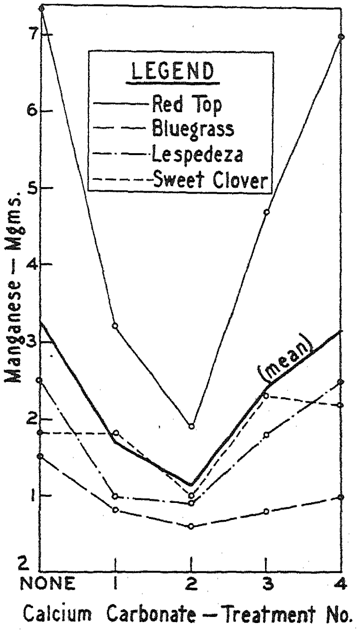
RESULTS

Results from calcium carbonate. The most noticeable result was the influence of the increasing amounts of calcium carbonate throughout the entire mass of soil (Treatments Nos. 1 and 2), as they reduced the percentage and the total amount of manganese in the crop; and the influence of the increasing degree of saturation of the surface soil layer by calcium (Treatments Nos. 3 and 4), as it had the very reverse effect. The percentages of the manganese in the crop are shown in figure 1, and the totals of it in figure 2. There is such a pronounced similarity between these two figures as to testify that the manganese responds as a decided nutritional disturbance in the plant metabolism rather than as a variation in manganese amounts simply according to variable plant mass. When the manganese behaviors, as given in figures 1 and 2, are related to the total calcium taken by the crop, as given in figure 3, then this fact becomes more evident. In Treatments Nos. 1 and 2 by limestone, which were lessening the soil acidity to greater degrees and were giving large calcium intake by the crop, there were decided decreases in the manganese concentrations of and intake by the crop. Yet in Treatments Nos. 3 and 4, which saturated the upper portion of the soil more completely so as to change the soil reaction much more in that limited soil volume and to deliver still greater amounts of calcium into the crop, there was the reverse relation between the manganese and the calcium, and gave increasing concentrations and total amounts of manganese taken by the crop.

This suggests clearly that an increase in the amounts of calcium carbonate throughout the soil, so as to shift its reaction toward neutrality, served to decrease the movement of manganese into the crop. Increasing the delivery of calcium to the plant by means of the higher saturation in the limited surface soil zone brought increasing delivery of manganese presumably from the remaining three-fourths of the soil given no calcium carbonate. As an agent that removed soil acidity, the calcium carbonate lessened the amount of manganese going from the soil to the crop. As a fertilizer that supplied calcium to the crop, it enabled the plants to take greater amounts of manganese from the soil below the zone of calcium fertilization.



1

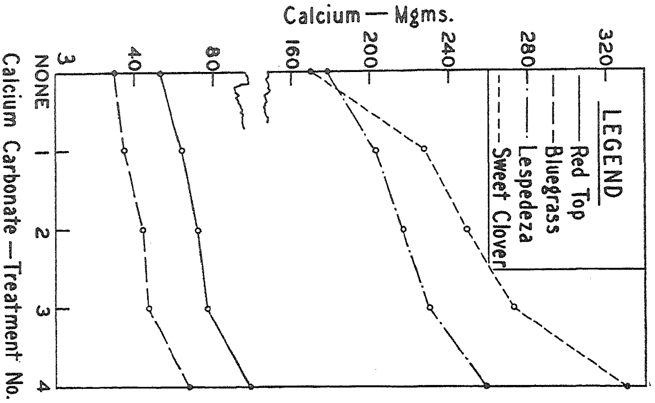


2

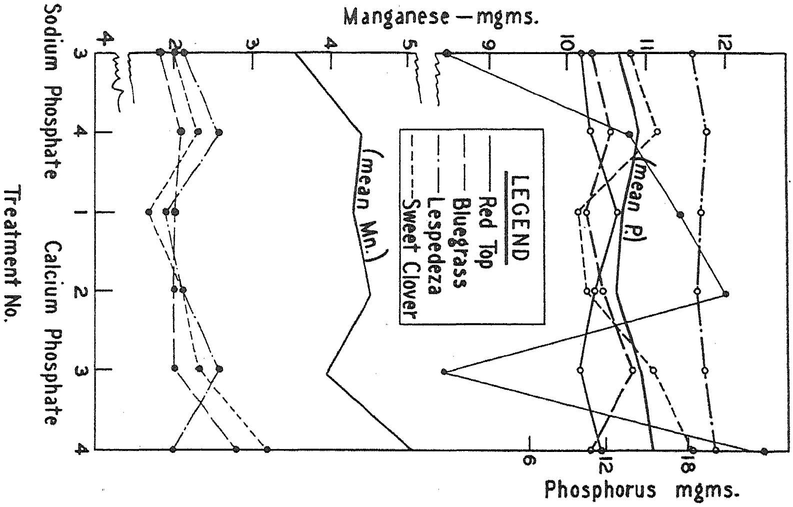
FIG. 1. Percentages of manganese in the different crops as influenced by two different amounts of calcium carbonate applied throughout the soil (Treatments Nos. 1 and 2), and into the surface soil only (Treatments Nos. 3 and 4). FIG. 2. Total manganese in the different crops as influenced by two different amounts of calcium carbonate applied throughout the soil (Treatments Nos. 1 and 2), and into the surface soil only (Treatments Nos. 3 and 4).

Possibly an increased or modified microbiological action as a competitor with the plant for the manganese (7, 10), may be the explanation for the reduction in manganese within the crop when calcium carbonate was distributed throughout the soil. This is suggested by the fact that the smaller application (Treatment No. 1), was relatively more disturbing than the larger one (Treatment No. 2), as is shown by the graph as the mean for all four crops either as percentage or as total manganese in figures 1 and 2. These studies did not aim to separate the microbial from the simple chemical effects.

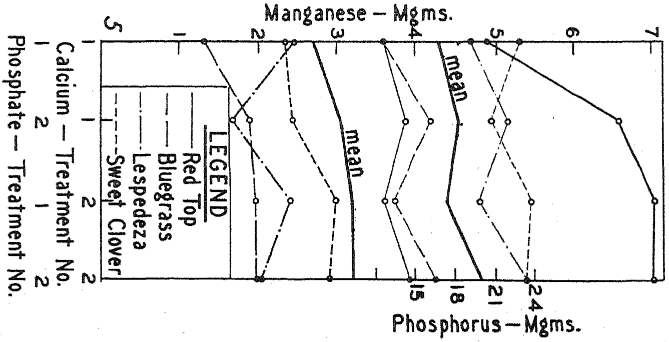
Such facts bring to attention the need to consider whether our use of calcium carbonate, or limestone, for the purpose of correcting soil acidity


Calcium — Mgms.
320
280
240
200
160
80
40
3
LEGEND
Red Top
Bluegrass
Lespedeza
Sweet Clover
NONE
1
2
3
4
Calcium Carbonate — Treatment No.

3


Manganese — mgms.
12
11
10
9
5
4
3
2
4
LEGEND
Red Top
Bluegrass
Lespedeza
Sweet Clover
(mean P.)
(mean Mn.)
Sodium Phosphate
3
4
Calcium Phosphate
1
2
3
4
Treatment No.
6
12
18
Phosphorus mgms.

4


Manganese — Mgms.
5
1
2
3
4
5
6
7
mean
mean
LEGEND
Red Top
Bluegrass
Lespedeza
Sweet Clover
Calcium — Treatment No.
1
1
2
2
Phosphate — Treatment No.
1
2
1
2
15
18
21
24
Phosphorus — Mgms.

5

is the most effective service by this soil treatment that is now undergoing wider adoption as a regular farm practice. They suggest that calcium must be put into the fertilizer category, and that excessive applications prompted by low cost or unbridled enthusiasm may bring disappointments.

Results from phosphates. The influence of the single phosphate soil treatments on the manganese intake into the crop was wholly positive, in that as more phosphate was given, either throughout the entire soil mass or into the surface soil only, there was increasing manganese in the harvest. These data are brought together in figure 4, which gives the totals for manganese and for phosphorus taken by the plants per pot.

Increasing the sodium phosphate in the upper soil portion increased the manganese taken. Putting the calcium phosphate into the top soil (Treatments Nos. 3 and 4), was more effective in bringing both manganese and phosphorus into the harvest. This is shown by the highest points on the graphs at the right side where the double dosage of calcium phosphate in the surface soil is indicated. The positive relation between the total manganese and the total phosphorus in the crop is shown more clearly by the close parallelism between the graphs representing the respective means for all crops. It points to an increase of manganese that was parallel with increased crop yield.

Results from calcium carbonate combined with calcium phosphate. When the joint applications of calcium carbonate and calcium phosphate are observed for their influence on the manganese harvested in the crop, this is slightly greater per unit of phosphorus taken by the crop than was the case where phosphates were applied singly. This is shown in figure 5, more particularly in the graph for the mean of all crops combined. The offering of more of each of these soil treatments so as to grow heavier crops increased the manganese taken from the soil. This suggests that the use of the manganese was correlated with the better or increasing growth through calcium and phosphate treatments.

Seemingly, then, the manganese was not a limiting factor in this Putnam silt loam. Its consumption by the plant from this soil was hindered, in some measure, by the phosphorus shortage, but more by the calcium shortage. It was when both calcium and phosphorus were applied that the largest

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Explanation of figures 3–5

FIG. 3. Total calcium in the different crops as influenced by two different amounts of calcium carbonate applied throughout the soil (Treatments Nos. 1 and 2), and into the surface soil only (Treatments Nos. 3 and 4). FIG. 4. Total manganese and phosphorus in the different crops as influenced by different amounts of phosphates applied throughout the soil (Treatments Nos. 1 and 2), and into the surface soil only (Treatments Nos. 3 and 4). FIG. 5. Total manganese and phosphorus in the different crops as influenced by two different amounts of calcium carbonate and calcium phosphate used in their possible combinations in the surface soil. (Lighter lines = P. Heavier lines = Ca.)

crops were grown, and that the larger amounts of manganese were taken from the soil.

Manganese contents of the different crops. The contents in manganese of the different crops are worthy of note. They are in agreement with analyses by others, particularly the high value for redtop (6, 14), and suggest that manganese is another help in fitting crops into the general ecological array of plants according to composition (4). The variations in concentrations and totals in the different crops are assembled in table 1.

TABLE 1

Concentrations and totals of manganese in the different crops.
(Ranges for different soil treatments)

Crops	Concentrations, per cent			Totals, mgms.		
	Soil treatments					
	Calcium carbonate	Phosphates	Calcium carbonate plus phosphate	Calcium carbonate	Phosphates	Calcium carbonate plus phosphate
Redtop	.023–.064	0.10 –0.14	.053–.071	1.9–7.0	0.8–1.3	4.9–7.0
Bluegrass	.008–.01	0.020–0.024	.013–.018	0.6–1.0	1.8–2.8	1.3–1.9
Lespedeza	.008–.017	0.014–0.018	.011–.016	0.9–2.5	1.9–2.6	1.7–2.4
Sweet clover	.012–.022	0.020–0.026	.014–.019	1.0–2.3	1.7–3.2	2.3–3.0
Range of variation in concentration	0.56	.016	.042			

In terms of concentrations of manganese within the crop, redtop is much the highest, reaching 0.14 per cent on soil given calcium phosphate only, and .071 per cent where this treatment was combined with calcium carbonate. It is followed in order by sweet clover with .026 per cent as maximum. Then comes bluegrass with .024 per cent as its highest and lespedeza with .018 per cent as its uppermost concentration of manganese in these trials. When the calcium carbonate was put into the surface soil to give more calcium to the crop, then the concentration of manganese was higher in the lespedeza than in the bluegrass.

When attention is directed toward the total manganeses in the crop, then the redtop is the highest, provided it was given calcium phosphate either singly or combined with calcium carbonate. Here in the case of a crop commonly considered suitable for lime-deficient soils and commonly not given soil treatment, calcium and phosphorus play an influential role in helping it to get manganese from the soil. Sweet clover follows in order as it did for manganese concentrations, particularly for the soil treatments of calcium carbonate and calcium phosphate used jointly. Bluegrass took the largest amounts for this crop when it was given phosphate, while lespedeza behaved similarly.

SUMMARY

The concentrations of manganese within the crop and the totals taken by it from the soil point to a dual role by calcium carbonate in relation to this micro-nutrient in plant nutrition. When calcium carbonate, or limestone, was mixed throughout the soil so as to modify its reaction, then the concentration and total of manganese in the crops were decreased as the application to the soil and the consumption of calcium by the crop increased. When, however, the application was put into the surface soil to increase crop consumption of the calcium even more, then the reverse effect on manganese was manifested, so that the concentration and the total of manganese were increased.

When phosphate was applied to provide increasing concentrations, whether in the entire or in the limited soil volume, then the additional phosphorus for the crop gave increasing manganese harvest, roughly parallel with increased crop growth.

Combinations of lime and phosphate in the limited soil areas aided the crop in taking more manganese.

These studies emphasize the need to consider the beneficial nutritional role of calcium within the plant, on soils such as the type used, in making manganese available for the plant as reflected in the increased concentrations. Then there is need to consider the possible detrimental role of calcium carbonate as it modifies the reaction of the soil or other soil conditions and reduces the manganese taken by the crop possibly to the danger point of manganese deficiency.

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CYLINDROCHYTRIDIUM JOHNSTONII GEN. NOV. ET SP. NOV., AND NOWAKOWSKIELLA PROFUSUM SP. NOV.

JOHN S. KARLING

(WITH SIXTEEN FIGURES)

During the Christmas holidays, 1940, while duck hunting on the Mount Prospect estate of J. Ambler Johnston which adjoins the Pamunky River in New Kent County, Virginia, I collected samples of water containing vegetable debris from a number of swamps and streams to determine the presence and relative abundance of chytridiaceous fungi during the winter months. These samples were brought to New York and placed in deep glass dishes on a table before an east window in the laboratories at Columbia University and baited with cooked, bleached leaf fragments, root tips, etc., of various grasses in the manner previously described by the author (1934, 1935, 1937). Within a fortnight a large number of fungi and chytrids appeared. The infected grass tissues were then washed thoroughly with distilled water under pressure and transferred to sterile Petri dishes containing charcoal water and bits of cellophane. The latter has proven to be an excellent medium for the growth of these chytrids, as Haskins (1939) has so well shown for other species.

Among the numerous fungi which were trapped in this manner appeared a few thalli of a monocentric chytrid with a cylindrical, stalked or septate sporangium subtended by an extensive catenulate rhizoidal system. Because of the characteristic shape of its sporangium, this chytrid was first believed to be a species of *Clavochytridium* Cox (1939) or *Blastocladiella* Matthews (1937), but subsequent observations showed that it differs from these genera by one outstanding and several minor characters. The sporangia of the two above-mentioned genera open by the deliquescence of one or more exit papillae, while those of our fungus are operculate. In addition, its zoospores include one large refringent globule like most other chytrids; those of *Clavochytridium* and *Blastocladiella* contain several minute refractive bodies and resemble the zoospores of other species of the Blastocladiales.

Because of its operculate, cylindrical, and stalked sporangia our species does not belong in either of these or any other known chytrid genera. A new genus is accordingly established to include this chytrid, and because of the characteristic shape of its sporangia the name *Cylindrochytridium* is proposed. The type species is named *C. Johnstonii* in honor of Mr. J. Ambler Johnston of Richmond, my kind and generous host on the occasion of this pleasant holiday in Virginia.

CYLINDROCHYTRIDIUM Karling, gen. nov.

Thallus monocentric and eucarpic. Zoosporangia usually stalked and cylindrical, occasionally sessile, operculate. Zoospores posteriorly uniflagellate, emerging fully formed and lying quiescent in a globular mass at the orifice of the sporangium for a few minutes before swimming away. Rhizoidal system extensive, branched with numerous catenulate spindle-shaped swellings. Resting spores unknown.

Thallo monocentrico, eucarpico; zoosporangiis plerumque stipitatis et cylindricis, aliquando sessilibus, operculatis. Zoosporis a tergo uniflagellatis, maturis emergentibus et globoso cumulo orificio sporangii quiescentibus atque mox natantibus. Rhizoideo systemate extenso et ramoso, cum numerosis catenulatis fusiformibus incrementis. Sporis perdurantibus incompertis.

Cylindrochytridium Johnstonii Karling, sp. nov. Zoosporangia hyaline, smooth, thin-walled, usually tubular, cylindrical or slightly clavate, 12–25 μ × 30–800 μ, occasionally oval, pyriform and sessile; stalk or basal portion usually of the same shape and diameter as the sporangium, but sometimes inflated, vesicular, irregular and apophysis-like. Operculum oval, ellipsoidal, 4 × 6 μ–8 × 10 μ, spherical, 4–17 μ; remaining attached to the sporangium or lying loose nearby. Zoospores spherical, 5.6–7 μ, with a large highly refractive globule; flagellum 22–26 μ long. Rhizoidal system arising

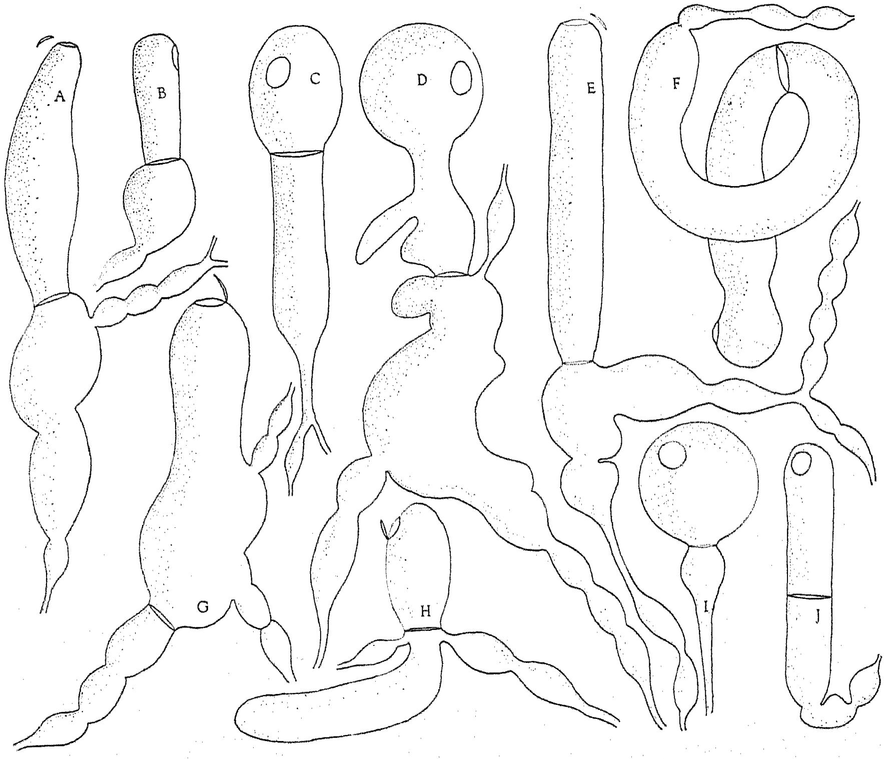


FIG. 1. *Cylindrochytridium Johnstonii.* Variations in the size and shape of sporangia.

from one to several points on the base of the stalk, extending over a radius of 100–1200 µ; spindle shaped swellings 8 × 12 µ–20 × 30 µ, rarely lacking entirely.

Saprophytic in decaying vegetable debris in swamps and streams in New Kent County, Virginia.

Fungus saprophyticus; zoosporangiis hyalinis, levibus, tenui pariete, plerumque tubulosis, cylindricis aut parum clavatis, 12–25 µ × 30–800 µ, interdum ovalibus, pyriformibus atque sessilibus; stipite aut radicali parte plerumque similiformi et -diametro sporangio, sed aliquando inflato, vesiculoso, irregulari et apophysiformi. Operculo ovali, ellipsoideo, 4 × 6 µ–8 × 10 µ, aut sporangio affixo aut liberato adiacente. Zoosporis sphaericis, 5.6–7 µ, magno maxime refractivo globulo praeditis; flagello 22–26 µ longo. Rhizoideo systemate aut uno aut pluribus locis radicali ex parte stipitis oriente, 100–1200 µ; incrementis fusiformibus 8 × 12 µ–20 × 30 µ, quae raro omnino desunt.

The sporangia of this species are predominantly tubular and cylindrical, but they may often vary considerably in shape, as is shown in figures 1A–1J. In some individuals the basal portion or stalk of the thallus may be very irregular (figs. 1A, 1D, 1E, 1G, and 1H), while in others the sporangia are curved and coiled with inflated tips (figs. 1F, 13, 14). Oval and obpyriform sporangia with short or elongate stalks may also occur (figs. 1C, 1I, 11, 12). When treated with choro-iodide of zinc, the walls become pale lavender in color, indicating a faint trace of cellulose. In this respect *C. Johnstonii* differs from *Clavochytridium stomophilum* and *B. simplex.*

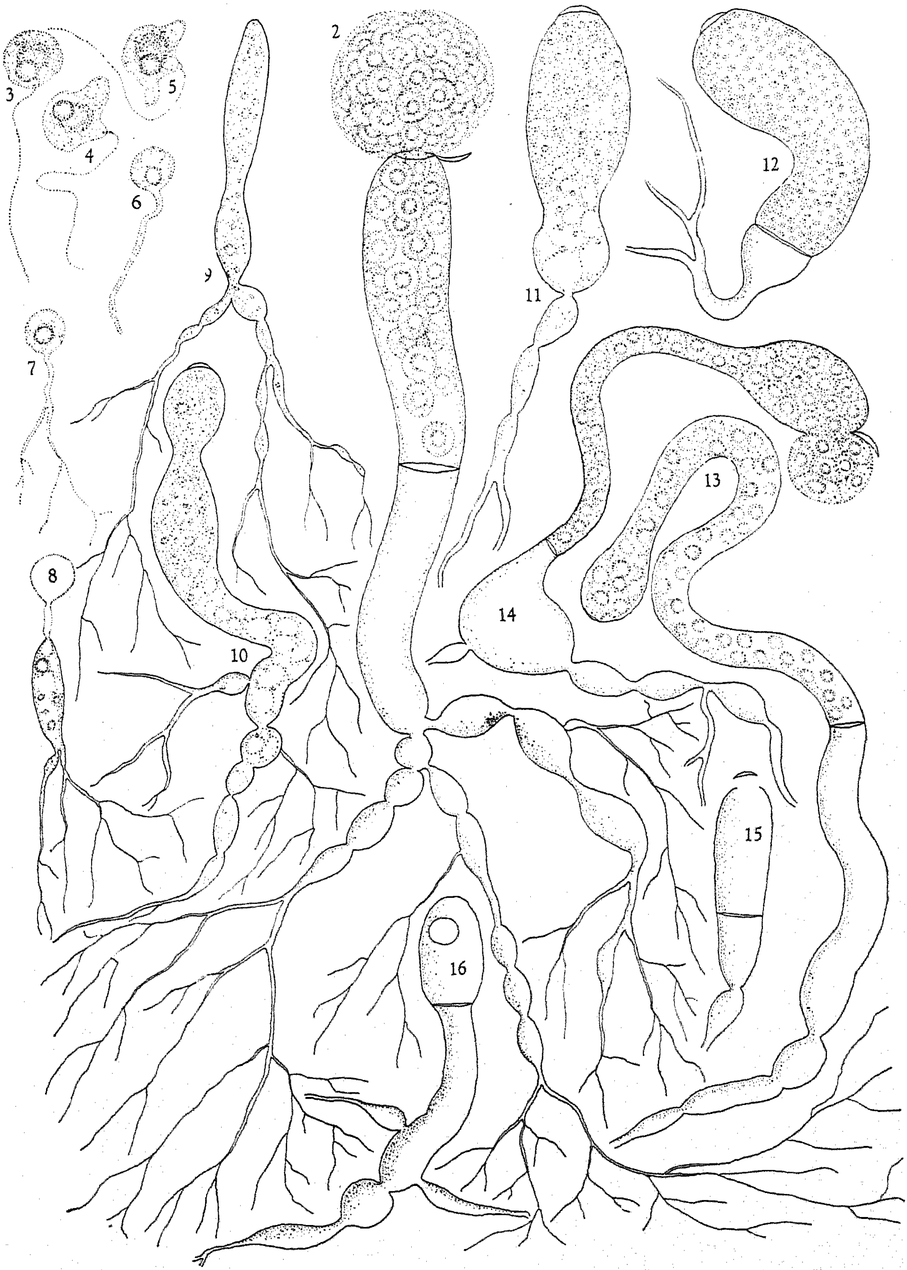
While the spindle-shaped swellings in the rhizoidal system are usually present, they may be lacking entirely in certain thalli (figs. 1C, 1I, and 12). These swellings were first believed to be due to the expansion of the rhizoids after they had passed through successive cell walls of the grass leaf, but this is apparently not the cause of their formation. In the elongate elements of the vascular strands as many as four swellings were present in a single host cell, which indicates that they are a fairly constant morphological character. The rhizoidal system of *C. Johnstonii* is very similar to that of *Catenochytridium* Berdan (1939) with its compound catenulate apophysis, with the exception that the swellings are usually more elongate and thin-walled. In this latter respect it is more like that of *Clavochytridium.* Whether or not the swellings in the rhizoids of *C. Johnstonii* are to be regarded as constituting a compound apophysis is obviously a matter of personal interpretation. Because of its monocentric, rhizidiaceous, eucarpic thallus, this species apparently belongs in the Rhizidiaceae as this family is now recognized. Since no resting spores have been found, its relation to the other genera of this family is not clear at the present time.

DEVELOPMENT OF THE THALLUS

The development of *C. Johnstonii* is essentially the same as that of most monocentric rhizidiaceous chytrids which Sparrow, Couch, Berdan, and others have previously described, and it would be superfluous to describe this process in detail again. The zoospores (fig. 3) are characteristic in shape and activity and possess the well-known large refractive globule and posterior flagellum. The active swimming period lasts from 20 minutes to two hours, during which the zoospores may become intermittently amoeboid (figs. 4, 5). In germination, a fairly thick germ tube is formed (fig. 6) which penetrates the host cell and soon branches once or several times (fig. 7). When the boiled grass tissues are very soft, and at the point of disintegration, the thalli may develop intramatrically, and in such cases the rudiments of the sporangium and stalk begin as an elongate swelling in the germ tube at or near the point of branching (fig. 8). As the swelling increases in size, the zoospore case and a portion of the germ tube eventually disappear. When the thallus occurs partially intra- and extramatrically, the zoospore and a part of the germ tube form the sporangium and stalk after the rhizoidal system has become fairly well established (figs. 9, 10).

As the thallus matures, the protoplasm slowly flows upward into the incipient stalk and sporangium, and as a result the rhizoids and lower portions become increasingly vacuolate (figs. 10, 11) in much the same manner as has been described by Cox for *Clavochytridium*. In the meantime the amount of refractive material has increased and appears in the form of glistening suspended globules, as is characteristic of most rhizidiaceous chytrids. After most of the protoplasm has aggregated in the upper part of the thallus, a cross wall is formed which delimits the sporangium proper from the more or less empty portion and rhizoidal system (fig. 12). After this, the protoplasm becomes coarsely granular in appearance (fig. 12), and in a few hours the large definitive refractive globules appear (fig. 13). Cleavage seems to occur during or shortly after the granular stage, but cleavage furrows are not conspicuous at any stage in living material. The sporangium may remain in the stage shown in figure 13 for several hours, but eventually the operculum is pushed up and the zoospores begin to emerge (fig. 14). The operculum is fairly large and may occur at the apex (figs. 2, 15, 1G, 1H, 1E, 1F) or subapically (figs. 1C, 1D, 1I, 1J, 1r, 16).

If the thallus occurs intramatrically in the soft host tissues, the tip of the sporangium usually projects to the surface so that the zoospores have no difficulty in getting out of the host. In some thalli, however, the zoospores may be liberated directly within the host. The zoospores emerge slowly en masse and are surrounded by a film of fairly consistent fluid or matrix (fig. 2), as in *Endochytrium, Chytridium, Nephrochytrium*, etc. Before all have emerged from the sporangium, the globular mass may break up and the individual zoospores swim away. Those which are left in the sporangium



FIGS. 2–16. *Cylindrochytridium Johnstonii;* showing the development of the thallus and sporangia.

then emerge one by one and swim directly away. In swimming, the zoospores of *C. Johnstonii* behave like those of most other chytrids, and nothing unusual in this respect has been observed. So far, no resting spores have been found, and it is impossible to say at present whether this species is homo- or heterothallic.

In the same host tissues with *C. Johnstonii* occurred another chytrid species which is characterized by an unusually coarse, profuse rhizomycelium and operculate zoosporangia. It is obviously a species of *Nowakowskiella* but differs in several ways from *N. elegans, N. ramosum,* and *Septochytrium variable,* and I am accordingly diagnosing it as a new species, *N. profusum.* An intensive cytological study of this species is now in progress, and the results thereof are to be published shortly.

Nowakowskiella profusum Karling, sp. nov. Rhizomycelium very profuse, extensive, and richly branched, hyaline, 6-15 μ in diameter; well-defined, septate, spindle-shaped and oval swellings rare or lacking; rhizoids abundant. Zoosporangia terminal or intercalary, hyaline, smooth, rarely apophysate, spherical, 10–45 μ, ovoid, ellipsoid, 8 × 12 μ–20 × 35 μ, clavate, obclavate, 10–22 μ × 15–40 μ, pyriform, obpyriform, elongate, cylindrical, 8 × 25–10 × 50 μ, lobed and irregular. Operculum apical, subapical or lateral, oval and spherical, 4.4 μ–7 μ, remaining attached to the sporangium or lying nearby. Zoospores hyaline, spherical, 4 μ–5.5 μ with a small refringent globule, 0.7–2 μ. Resting spores terminal or intercalary, spherical, 14–25 μ, ovoid, ellipsoid, 10 × 15 μ–14 × 22 μ, truncate, spindle-shaped, and rarely irregular, with a fairly thick, yellowish-brown, smooth wall; content granular with numerous refractive globules; germinating after a short rest period; forming one or two broad, tapering, thin-walled, operculate exit tubes and producing zoospores directly within; or content of spores occasionally growing out and forming a thin-walled zoosporangium on the surface.

Saprophytic in decaying vegetable debris in swamps and streams in New Kent County, Virginia.

Fungus saprophyticus; rhizomycelio maxime profuso, extenso, copiose ramoso, hyalino, 6–15 μ diametro; incrementa definita, septata, fusiformia, ovalia raro habente aut deficiente; rhizoidibus numerosis. Zoosporangiis terminalibus aut intercalaribus, hyalinis, levibus, raro apophysatis, sphaericis, 10–45 μ, ovoideis, ellipsoideis, 8 × 12 μ–20 × 35 μ, clavatis, obclavatis, 10–22 μ × 15–40 μ, pyriformibus, obpyriformibus, elongatis, cylindricis, 8 × 25 μ–10 × 50 μ, lobulatis et irregularibus. Operculo apice aut sub apice aut a latere formato, ovali et sphaerico, 4.4 μ–7 μ, aut sporango affixo aut prope adiacente. Zoosporis hyalinis, sphaericis, 4–5.5 μ, parvo refringente globulo (0.7–2 μ) praeditis. Sporis perdurantibus terminalibus aut intercalaribus, sphaericis, 14–25 μ, ovoideis, ellipsoideis, 10 × 15 μ–14 × 22 μ, truncatis, fusiformibus, et raro irregularibus cum potius crasso, sucineo colorato, levi pariete; contentis granulatis cum permultis refractivis globulis; germinatione post brevem quietem confecta; unum (interdum duo) latum acuminatum, tenui pariete, operculatum tubulum exeuntem gignentibus, zoosporis intra evolventibus, aut contentis sporae interdum emergentibus ut sporangium tenuis parietis in superficie fiat.

That chytridiaceous fungi may occur abundantly during the winter months in Virginia is shown by the large number of additional species which were found in the water and vegetable debris from New Kent County. In addition to the two new species described above, the following known species were found: *Sphaerita* sp. in *Euglena* sp., *Rhizophidium carpophilum* on *Saprolegnia* sp., *R. globosum* on *Cladophora glomerata*, *Endochytrium operculatum*, *Rhizophlyctis Peterseni*, *Catenochytridium carolinianum*, *Nephrochytrium aurantium*, *Cladochytrium replicatum*, *C. tenne* (?), *C. hyalinum* (Berdan, in press), *Septochytrium variable*, and *Nowakowskiella elegans*. All these species are new for Virginia, as far as I am aware.

SUMMARY

Cylindrochytridium Johnstonii is a new monocentric, eucarpic, rhizidiaceous, saprophytic species of the family Rhizidiaceae and occurs in swamps and streams containing vegetable debris in New Kent County, Virginia. It is usually characterized by an elongate tubular, cylindrical or slightly clavate sporangium, an extensive rhizoidal system with numerous catenulate, spindle-shaped swellings, and spherical, posteriorly uninflagellate zoospores with a large refringent globule. Resting spores are unknown.

Nowakowskiella profusum is characterized by a coarse, profuse rhizomycelium, terminal or intercalary zoosporangia which are quite variable in size and shape, and yellowish-brown terminal or intercalary resting spore.

In addition to these new species, eleven other chytrids were isolated from water samples from New Kent County, Virginia.

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CYTOLOGICAL STUDIES IN LACTUCA

THOMAS W. WHITAKER AND ROSS C. THOMPSON

(WITH NINE FIGURES)

This report presents a series of cytological observations of certain interspecific hybrids in the genus *Lactuca*. Previous papers have been concerned with the cytology of the various species, and the genetic aspects of interspecific hybridization in this genus (Whitaker and Jagger 1938, Thompson *et al.*, in press). As far as the available material would permit, the genetic and cytological variability of the species in the genus have been explored with the object of locating suitable material for hybridization with cultivated lettuce (*L. sativa*). Incidentally, observations have been made which we consider contribute to a better understanding of relationships between the several species studied, and we have obtained evidence which throws some light on the evolutionary processes at work within the genus.

The present paper constitutes a joint report of certain work of the past several seasons at the U. S. Horticultural Station, Beltsville, Maryland, and the U. S. Horticultural Field Station, La Jolla, California. It is primarily concerned with the cytological aspects of the problems enumerated above.

MATERIALS AND METHODS

There were available for study interspecific hybrids of the following species: *Lactuca tatarica* (L.) C. A. Mey. × *L. indica* L.; *L. Raddeana* Maxim. × *L. indica; L. sativa* L. × *L. virosa* L.; *L. tatarica* × *L. floridana* (L.) Gaertn. *L. graminifolia* Michx. × *L. indica; L. graminifolia* × *L. tatarica; L. graminifolia* × *L. virosa; L. graminifolia* × *L. floridana; L. canadensis* L. × *L. floridana* (for sources of material see Thompson *et al.*, in press). Buds in which the pollen mother cells had initiated meiosis were fixed in an acetic acid–absolute alcohol mixture, and prepared as described elsewhere (see Jagger and Whitaker 1937). The cytological observations have necessarily been limited to those crosses which have produced material suitable for meiotic studies.

OBSERVATIONS

L. Raddeana (9)[1] × *L. indica* (9). Plants obtained from this cross had 9 pairs of chromosomes. There was good synapsis between the two sets of chromosomes at diakinesis (fig. 1). In the course of the work several hundred cells have been observed, but none gave any evidence of irregularities at meiosis. Homology between the two genoms is substantiated by the fact that the hybrid produced viable seed if harvested at the proper time. It should be pointed out that there were disturbances in the hybrid plants which were not reflected in gross cytological aberrations. For example, the seed produced by the F_1 was viable only if harvested prematurely; if allowed to mature the embryos became shriveled, shrunken, and would not germinate.

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[1] The figures in parentheses immediately following the specific names are the *n* chromosome numbers of the species.

L. tatarica (9) × *L. indica* (9). Hybrids of this mating had 18 somatic chromosomes. Meiotic observations indicated that the two genoms are not completely homologous. Typical cells have 7 bivalents and 4 univalents (fig. 2). There were no instances of multivalent association and 8 was the maximum number of bivalents observed. Chromatin bridges, and unpaired and fragmented chromosomes were observed. As might be expected from these cytological observations, the F_1 was entirely sterile.

L. sativa (9) × *L. virosa* (9). The F_1 plants resulting from this cross had 18 somatic chromosomes. Synapsis between the chromosomes of the genoms was not complete. Frequently the members of a pair, or less frequently, the members of two pairs of bivalents remained unconjugated (fig. 3). Chromatin bridges were of frequent occurrence at IA (fig. 4), interkinesis, and IIA. Numerous fragments were observed; most of them appeared to be acentric and were lost in the cytoplasm. These disturbances at meiosis were sufficient to cause a high degree of sterility. Three per cent of the pollen were viable. However, not a single seed was obtained from the four plants grown to maturity.

L. tatarica (9) × *L. floridana* (17). This mating was successful and produced 7 plants, all of which appeared to be interspecific hybrids. It represents a successful case of fertilization in which the female parent, *Lactuca tatarica*, is diploid, and the pollen parent, *L. floridana*, is an amphidiploid.

The F_1 plants from this cross had 26 somatic chromosomes. Cells satisfactory for the determination of pairing relationships were observed to have a variable number of bivalents. There were never less than 9 and infrequently as many as 11 bivalents (fig. 5), and occasional trivalents have been observed. In addition to the above features, there were such meiotic irregularities as unpaired chromosomes, chromatin bridges, and fragments.

From the type and quantity of the irregularities found at meiosis, one could safely predict that the F_1 plants would be sterile. Such was the case, although they were vigorous vegetatively, and produced an abundance of flowers; there were no viable achenes.

L. graminifolia (17) × *L. indica* (9). The F_1 plants from this mating had 26 chromosomes in root tip cells. In our observations of meiosis we have counted a maximum of 7 bivalents per cell. The remaining chromosomes are unpaired, and apparently distributed at random during the first division. These cytological irregularities did not result in complete sterility in the F_1 plants. A few seed were obtained late in the flowering season.

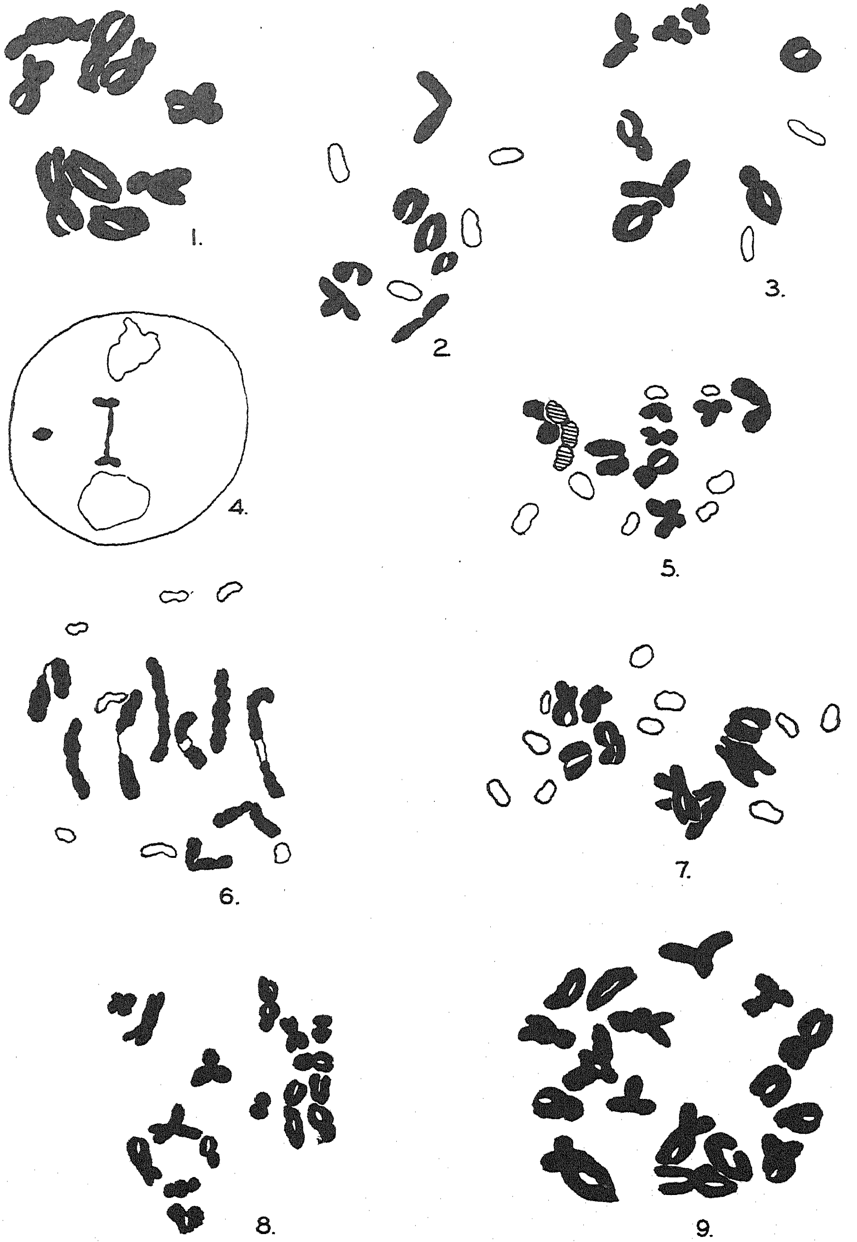

FIG. 1. Diakinesis, *Lactuca Raddeana* × *L. indica*, showing 9 bivalents. FIG. 2. Diakinesis, *L. tatarica* × *L. indica*, showing 7 bivalents, the 4 univalents are drawn in outline. FIG. 3. Diakinesis, *L. sativa* × *L. virosa;* 8 bivalents, 2 univalents. FIG. 4. Late telophase, *L. sativa* × *L. virosa*, showing chromatin bridge and acentric fragment. FIG. 5. Diakinesis, *L. tatarica* × *L. floridana;* 1 trivalent (crosshatched), 8 bivalents, and 7 univalents. FIG. 6. First anaphase, *L. graminifolia* × *L. virosa;* 9 bivalents, 8 univalents. FIG. 7. Diakinesis, *L. graminifolia* × *L. tatarica;* 8 bivalents, 10 univalents. FIG. 8. Diakinesis, *L. graminifolia* × *L. floridana;* 17 bivalents. FIG. 9. Diakinesis, *L. canadensis* × *L. graminifolia;* 17 bivalents.

L. graminifolia (17) × *L. virosa* (9). Although this mating was attempted on numerous occasions only one hybrid plant was obtained. The F_1 plant had 26 chromosomes (fig. 6). Pairing was of the *Drosera* type, 9 bivalents plus 8 univalents. There were many irregularities, for example chromatin bridges at IA, and IIA, fragments and even entire chromosomes lost in the cytoplasm. Because of the great number of cytological irregularities we anticipated considerable pollen sterility. Such was the case; only about 9 per cent of the microspores indicated viability by the staining method and no viable seed developed.

L. graminifolia (17) × *L. tatarica* (9). The F_1 plants of this combination had 26 chromosomes. Meiosis in the hybrid was very irregular. Lagging

TABLE 1

Summarized cytological observations of species hybrids in Lactuca

Species	Chromosome number of F_1		Per cent viable pollen	Production of seed	Pairing	Cytological irregularities
	n	2n				
L. Raddeana (9) × *L. indica* (9)	9	18	16.6	Fair	9^{II} Complete pairing	None
L. tatarica (9) × *L. indica* (9)		18	—	None	$2\text{–}4^{\mathrm{I}}$ $7\text{–}8^{\mathrm{II}}$	Non-pairing Bridges Fragments
L. sativa (9) × *L. virosa* (9)	9	18	3.0	None	$1\text{–}2^{\mathrm{I}}$ $7\text{–}8^{\mathrm{II}}$	Non-pairing Bridges
L. tatarica (9) × *L. floridana* (17)		26	14.9	None	$5\text{–}7^{\mathrm{I}}$ $8\text{–}9^{\mathrm{II}}$ 1^{III}	Univalents Non-pairing Bridges Fragments
L. graminifolia (17) × *L. indica* (9)		26	37.9	Few	$12\text{–}14^{\mathrm{I}}$ $6\text{–}7^{\mathrm{II}}$	Unpaired chromosomes
L. graminifolia (17) × *L. virosa* (9)		26	9.0	3 seeds	8^{I} 9^{II}	Bridges Fragments Unpaired chromosomes
L. graminifolia (17) × *L. tatarica* (9)		26	—	None	10^{I} 8^{II}	Bridges Fragments Unpaired chromosomes
L. graminifolia (17) × *L. floridana* (17)	17		90.0	Good	17^{II}	Occasional fragment and bridge
L. canadensis (17) × *L. floridana* (17)	17		9.0	Fair	17^{II}	None

chromosomes, unpaired chromosomes, and chromatin bridges were observed. In cells satisfactory for the observation of pairing relationships there were 8 bivalents and 10 unpaired chromosomes (fig. 7). No viable seed was obtained.

L. graminifolia (17) × *L. floridana* (17). The F_1 plants from this cross between two amphidiploid species had 17 pairs of chromosomes (fig. 8). At diakinesis all chromosomes were associated as bivalents. Multivalent association appeared to be rare or entirely lacking. A few fragments and an occasional chromatin bridge have been observed. Pollen counts indicated between 90 and 95 per cent good pollen. These hybrids were expected to be only slightly less fertile than the parents, and this was actually the case.

L. canadensis (17) × *L. floridana* (17). Hybrids from this mating had 17 pairs of chromosomes. The chromosomes were associated as bivalents in all the cells satisfactory for the determination of pairing relationships (fig. 9). A careful search through our material has not revealed a single cytological irregularity.

In table 1 the pertinent observations on the cytology of the F_1 plants of various *Lactuca* species described in detail have been summarized.

DISCUSSION

On the basis of the genetic and cytological evidence the amphidiploid species of *Lactuca* with 17 chromosomes form a closely related group. In fact the evidence suggests the theory that these species are derivatives of a single amphidiploid, i.e., the chromosome complement of the group may be represented by the formula *AABB*, where $A =$ the 8 chromosome genom and $B =$ the 9 chromosome genom. Facts supporting this statement are as follows.

1. Of the five crosses reported between species with seventeen chromosomes, four have produced F_1 plants that were partly or wholly fertile. It is true that there is considerable variation in fertility between the extreme case of *L. graminifolia* × *L. canadensis*[2] in which the F_1 is as fertile as either parent and the situation in the hybrids of the mating between *L. canadensis* × *L. floridana* in which only a few seed have been obtained. In only one cross was the F_1 sterile (*L. spicata* × *L. graminifolia*). However, the fact that the mating was successful is some indication of relationship.

2. In the F_1 plants that have been studied cytologically there is very good synapsis between the genoms of the parental species. Pairing in most crosses takes the form of bivalent association. We have observed very few multivalent configurations in interspecific crosses in this group of species.

3. In at least one cross (*L. canadensis* × *L. graminifolia*) which has been studied intensively it has been possible to demonstrate that specific differ-

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[2] Unpublished data in files of the writers.

ences are dependent upon relatively few gene differences (unpublished data on F_2, F_3, etc., of *L. canadensis* × *L. graminifolia*).

4. The 17-chromosome species of *Lactuca* are indigenous to eastern North America, from Canada to Florida. The fact that they are confined to this limited geographical area would seem to be another indication of close affinity.

It may be argued that the American species of *Lactuca* instead of being amphidiploids have descended from a single 9-chromosome tetraploid *Lactuca* species through the loss of one pair of chromosomes. Circumstantial evidence is against this supposition, because (a) in *L. sativa,* tetraploids produced by colchicine have been extremely sterile, probably as the result of relatively large amount of multivalent association (unpublished data); (b) on the contrary, the American species are very fertile (90–95 per cent good pollen), and any exception to bivalent association is rare.

The possibility that the American amphidiploids are the result of a mating between two 9-paired species and subsequent amphidiploidy with the loss of one pair of chromosomes cannot be entirely dismissed. However, there is no precedent on record for this type of origin, and it is to be expected that the loss of one pair of chromosomes would create serious difficulties interfering with viability.

If full consideration is given to their compatibility relationships and cytological behavior, it is probable that the 17-chromosome amphidiploid species of *Lactuca* have originated from a single occurrence of amphidiploidy. Speciation on the basis of this assumption has taken place through the accumulation of a number of relatively simple gene mutations, with perhaps some structural rearrangement of the chromosomes, since an occasional chromatin bridge has been found in certain crosses.

Having disposed of the question of genetic affinity between the American amphidiploid species of *Lactuca,* it now seems proper to review some of the evidence regarding their origin, that is, to consider which of the 8- or 9-chromosome species are the most likely ancestors of the American amphidiploids. We have no observations that would indicate the 8-chromosome parental species; on the other hand there are some data which suggest the group from which the 9-chromosome species may have come.

On the basis of genetic evidence, and with certain exceptions, the species of *Lactuca* fall into three compatibility groups (Thompson *et al.*, in press). Group I consists of the 9-chromosome species which are more or less closely related to cultivated lettuce (*L. sativa, L. Scariola, L. altaica, L. virosa, L. saligna*). Group II is made up of the following 9-chromosome species: *L. indica, L. Raddeana,* and *L. tatarica.* Group III is composed of the 17-chromosome American species. Of the 14 successful crosses obtained between members of two of these groups (groups II and III), three have been examined cytologically. In most crosses at least 8 chromosomes from each genom seemed to be homologous. Only one hybrid plant was obtained in hundreds of attempts to hybridize species in group I with the 17-chromosome American species (group III). In this hybrid pairing was of the *Drosera* type, indicating homology between 9 chromosomes of each genom. On the basis of pairing relationships the evidence is not sufficient to be decisive between group I and group II. It is clear from the genetic data that species hybrids are much more easily obtained in matings of the American amphidiploids with group II, and this may mean that the American amphidiploids find their closest affinity with members of this group. We have been informed that the morphological evidence also supports this conclusion, namely, that group III has many more characteristics in common with group II than with group I.[3]

SUMMARY

Observations of the principal details of meiosis in nine F_1 hybrids produced from a series of interspecific matings in *Lactuca* are reported. Three of these crosses were between species with 9 pairs of chromosomes, four between species having 9 and 17 pairs of chromosomes, and two between species with 17 chromosomes. Pairing behavior and irregularities are analyzed in these hybrids. It is evident from this analysis that the 9-chromosome species consist of at least two distinct compatibility groups. The 17-chromosome group is very homogenous. It is suggested that the latter group of species has descended from a single amphidiploid or may have resulted from a single occurrence of amphidiploidy.

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[3] Private communication from Dr. G. L. Stebbins, Jr., University of California, Berkeley, California.

"MULTINUCLEATE" PLANT CELLS

Paul R. Burkholder and Ilda McVeigh

(WITH ONE FIGURE)

During a study of the growth of some maize lines and hybrids, an apparent multinucleate condition was observed so frequently in cross sections of stems that we were led to investigate the real nature of the condition.

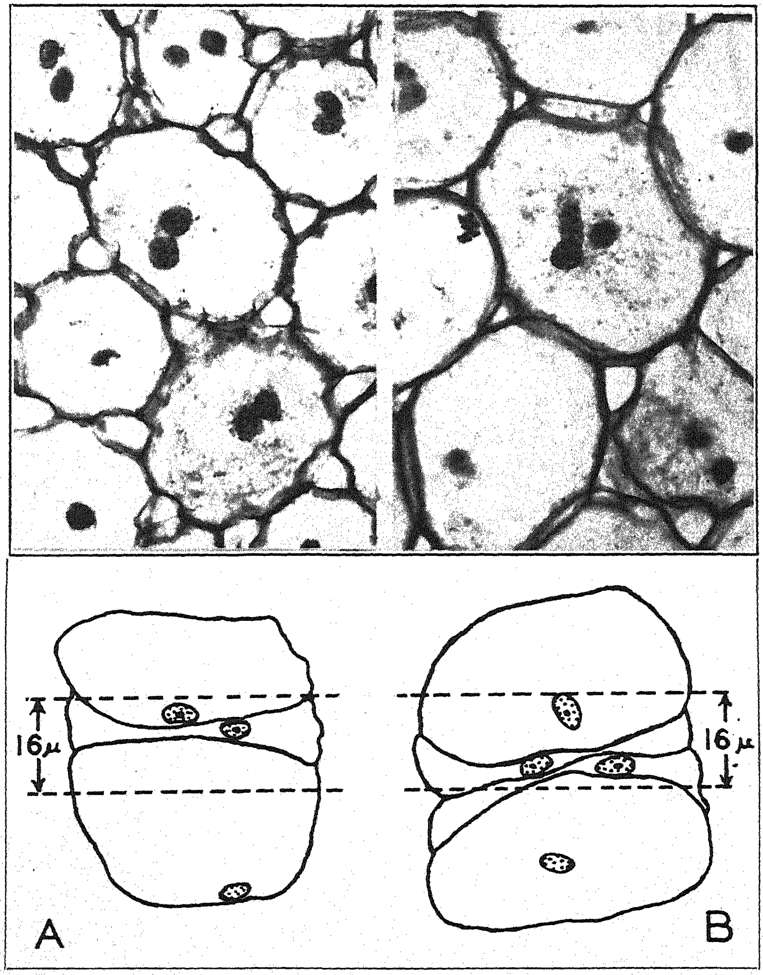

FIG. 1. Above: Transverse sections through internodes of young maize plants showing apparently bi- and trinucleate condition in ground parenchyma. Below: Diagrams of longitudinal sections through internodal parenchyma cells showing in A how cross sections cut 16 microns thick along dotted lines would give an apparently binucleate structure, and in B a trinucleate artifact.

Some workers with whom the phenomenon was discussed expressed the opinion that our inbred lines might be unique in possessing as a general rule multinucleate cells. Others confirmed our observations in the light of their own experiences with maize, and recalled that just one score years ago Beer and Arber (1920) had described multinucleate cells in 177 species representing 60 families of plants. Wipf and Cooper (1940) have since reported binucleate cells occasionally present in the cortical parenchyma of roots of eight species of leguminous plants. Even though a recent paper by Wareham (1936) exposed the fallacy of a so-called "multinucleate phase" in stem development, it appears that many botanists are not yet certain about the condition in parenchyma cells.

Further studies were made on both transverse and longitudinal sections through internodal tissue just above the intercalary meristem of a number of selected lines of maize. Microchemical tests with iodine, crystal violet, ninhydrin, Feulgen reagent, etc., convinced us that the small bodies grouped in the cells were really nuclei, and not starch grains or other debris. In both transverse and longitudinal sections appropriate tests with I–KI and sulphuric acid, and with ruthenium red, permitted clear demonstration of cell walls separating the nuclei, one to each cell. No apparent multinucleate condition was ever noted in longitudinal section. The alleged bi- and trinucleate conditions portrayed in the accompanying photomicrographs (fig. 1) are explained in the lower part of the figure by camera lucida drawings of cells in longisectional view. Many cells of the ground parenchyma adjacent to the meristem are compressed and distorted out of ordinary shape as a result of differential cell expansion in the internode. It is plainly seen how cross sections cut 16 microns thick (dotted lines) can produce multinucleate artifacts. Though the multinucleate condition is known to occur in special instances in the plant kingdom, it is not the true condition in stem parenchyma of maize. This brief note, therefore, substantiates the work of Wareham, who reported that cells of pith and cortex appearing multinucleate in cross section are in reality uninucleate.

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STUDIES OF PACIFIC ISLAND PLANTS—I

A. C. SMITH

This paper is the first of a series in which it is proposed to discuss new and noteworthy plants from the Pacific area and to revise limited groups of plants as the occasion arises. The geographic area under consideration includes the Polynesian, Micronesian, and Melanesian groups, although the Solomon Islands, being floristically so intimately related to New Guinea, may as a rule be excluded from treatment in this series. A substantial volume of herbarium material has recently been collected in the Pacific, and it seems probable that in the near future additional material will be available for study. The writer has no wish to intrude upon the fields of various students who are occupied with special taxonomic groups or geographic areas in the Pacific, and intends to limit this series to discussions of more or less neglected groups.

THE PACIFIC SPECIES OF MYRISTICA

In his treatment of the Myristicaceae, Warburg (Nova Acta Acad. Leop.-Carol. **68**: 1–680. *pl. 1–25.* 1897) definitely recognized only three species of *Myristica* in the Pacific, but subsequent collections indicate the existence of eight species, of which one is first described in the present paper. These species occur from Samoa and Tonga westward and are well localized, only one (*M. inutilis*) being known from several major geographic groups. They are distributed as follows: Samoa (2 species), Tonga (1 or possibly 2 species), Fiji (4 or possibly 5 species), New Hebrides (2 species), Carolines (1 species). In the neighboring Solomon Islands, 8 species are known (see A. C. Smith, Jour. Arnold Arb. **22**: 60–80. 1941), and in view of this it seems unlikely that only 2 species actually exist in the New Hebrides; it is to be anticipated that future collectors in this group will discover other species. The distribution of *Myristica* is an interesting illustration of the increasing paucity of species toward the east, as compared with the wealth of species in New Guinea, where at least 34 are now known. The insular species show strong affinities with those of New Guinea, some of them being more closely allied to Papuan relatives than to each other.

Since the Pacific species were originally described, for the greater part, from inadequate material, it seems advisable to include in this treatment descriptions based on the available specimens, except for *M. macrantha*, since the publication of which no additional material has become available. I have been privileged to see the specimens deposited in the following herbaria: Arnold Arboretum (A), Gray Herbarium (GH), New York Botanical Garden (NY), U. S. National Herbarium (US), the place of deposit being indicated by the abbreviations in parentheses. I am indebted to the directors and curators of the named institutions for the opportunity to examine specimens.

Several characters in the genus *Myristica* have a diagnostic value which has been neglected. The leaf-blades of the Pacific species are often ceriferous beneath, the wax being deposited either as a uniform thin layer or in minute crowded globules. The latter type is illustrated by *M. macrantha* and *M. castaneaefolia*. The type of pubescence on the staminate inflorescence is also a constant character and must be resorted to for the accurate separation of certain species. More obvious characters, such as leaf-proportions and size, venation, type of inflorescence, shape of perianth, and proportions of fruit are also fairly dependable. Leaf-shape, however, is often not a reliable character and hardly seems to justify specific separation unless it is supported by other evidence.

KEY TO THE PACIFIC SPECIES

Staminate inflorescence coarsely vermiform, simple or forked near base, the rachises densely cicatricose to base, 4 mm. or more in diameter; perianth cylindric-ellipsoid or campanulate, about twice as long as broad; connective slightly exceeding the anthers; lower surface of leaf-blades farinose- or papillose-ceriferous; Fiji.

  Leaf-blades large, 35–60 cm. long, 12–23 cm. broad, rounded to cordate at base; secondary nerves 24–35 per side; rachis about 10 mm. in diameter; perianth about 10 mm. long .... 1. *M. macrantha.*

  Leaf-blades smaller, (10–) 15–32 cm. long, (4.5–) 6–14 cm. broad, obtuse to rounded at base; secondary nerves 17–27 per side; rachis 4–5 mm. in diameter; perianth 5–7 mm. long .... 2. *M. castaneaefolia.*

Staminate inflorescence comparatively slender, the rachises rarely exceeding 4 mm. in diameter, the primary (and often secondary) peduncle usually obvious; lower surface of leaf-blades often ceriferous but smoothly so (rarely in no. 5 farinose-ceriferous).

  Leaf-blades persistently pale-tomentellous beneath; staminate perianth urceolate-cylindric, at least twice as long as broad; androecium-stalk nearly as long as anthers, the connective obviously produced; fruit oblong-ellipsoid, much longer than broad; Samoa to New Hebrides (and Solomons) .... 3. *M. inutilis.*

  Leaf-blades glabrous, at least at maturity; staminate perianth 1–2 times as long as broad; androecium-stalk conspicuously shorter than anthers, the connective not (or faintly) produced.

    Staminate inflorescence simple, the peduncle 1–1.5 mm. in diameter, swollen distally, the perianth campanulate, nearly twice as long as broad; leaf-blades comparatively small (6–15 cm. long, 2.5–6.5 cm. broad), inconspicuously ceriferous and concolorous, the secondary nerves inconspicuous; Fiji .... 4. *M. chartacea.*

    Staminate inflorescence usually obviously forked, the peduncle 1.5–4 mm. in diameter, the rachises usually elongate, the perianth subglobose or broadly campanulate, nearly as broad as long; leaf-blades larger (12–35 (–45) cm. long, (4–) 6–16 cm. broad), conspicuously ceriferous and usually glaucous beneath, the secondary nerves obvious, strongly prominulous beneath.

      Leaf-blades about twice as long as broad, the secondary nerves comparatively crowded; staminate inflorescence tomentellous (hairs several-celled, the lower cells conspicuously transversely fusiform); anthers 11–18; fruit ellipsoid (37–50 mm. long, 23–30 mm. broad); Carolines .... 5. *M. insularis.*

Leaf-blades usually 3–4 times as long as broad, the secondary nerves comparatively spaced; anthers 7–11.

Staminate inflorescence strigose (hairs simple or obscurely plumulose near base); fruit broadly ellipsoid or subglobose (28–40 mm. long, 24–30 mm. broad); Samoa and Tonga .... 6. *M. hypargyraea.*

Staminate inflorescence tomentellous (hairs branched from or near base, tangled); fruit oblong-ellipsoid, conspicuously longer than broad (37–50 mm. long, 23–28 mm. broadly); Fiji .... 7. *M. Gillespieana.*

Species of this relationship; leaf-blades chartaceous, obscurely ceriferous; inflorescence lacking; fruit essentially subglobose (27–32 mm. in diameter); New Hebrides 8. *M. Guillauminiana.*

1. MYRISTICA MACRANTHA A. C. Smith, Bishop Mus. Bull. **141**: 67. *f. 33.* 1936.

The original description was based on the material cited below and therefore does not need amplification.

Distribution: Fiji, known only from Vanua Levu at elevations up to 700 m.

FIJI—VANUA LEVU: Mbua, lower Wainunu River valley, *Smith 1719* (GH, NY—TYPE, US); Thakaundrove, southwestern slope of Mount Mbatini, *Smith 613* (GH, NY, US).

Common name: Male wangga.

The species is closely related only to *M. castaneaefolia,* being readily separable by the great size of all its parts. While this difference may not be very dependable as regards foliage, it is very striking in a comparison of the staminate inflorescences and perianths.

2. MYRISTICA CASTANEAEFOLIA A. Gray, Bot. U. S. Expl. Exped. **1**: 32. 1854; A. DC. in DC. Prodr. **14**: 193. 1856; Seem. Fl. Vit. 205. 1867; Warb. Nova Acta Acad. Leop.-Carol. **68**: 492 (as *M. castaneifolia*). *pl. 18.* 1897.

Tree to 18 m. high, the vegetative parts essentially glabrous throughout, the branchlets stout, subterete, soon cinereous and rugulose; petioles stout (1.5–5 mm. diam.), 12–35 mm. long, brownish or nigrescent, shallowly canaliculate; leaf-blades chartaceous or thin-coriaceous, oblong-elliptic, (10–) 15–32 cm. long, (4.5–) 6–14 cm. broad, obtuse or rounded at base, obtuse or obtusely cuspidate at apex, slightly reflexed at margins, dark brown above, glaucous beneath and farinose- or papillose-ceriferous (rarely smoothly ceriferous when young), the costa conspicuously raised above, prominent beneath, the secondary nerves 17–27 per side, spreading, straight, anastomosing near margins, impressed or faintly raised above, prominent beneath, the veinlets obscure, sometimes faintly impressed above and prominulous beneath; staminate inflorescence coarsely vermiform, up to 25 mm. long, usually forked near base, the peduncle stout (about 4 mm. in diameter), 1–6 mm. long, the secondary peduncles none, the rachises stout (4–5 mm. in diameter), very densely cicatricose, pubescent distally, the bracts ovate, minute, caducous; flowers aggregated toward ends of rachises, densely ferruginous-strigose or -sericeous (hairs about 0.7 mm. long, simple or obscurely plumulose near base), the pedicels very short, the bracteole deltoid-ovate, 1–1.5 mm. long, subacute; perianth thick-carnose, cylindric-ellipsoid, 5–7 mm. long, 2.5–3.5 mm. in diameter, the lobes 3, deltoid-oblong, subacute, about 1 mm. long; androecium 4–5 mm. long, the stalk stout, 1–1.5 mm. long, shortly castaneous-strigose near base, the anthers 8–10, 2.5–3.5 mm. long, the connective stout, obtuse and slightly (0.2–0.5 mm.) projecting at apex; fruit subsessile at ends of short inflorescences, ellipsoid or ovoid-ellipsoid, often inaequilateral and obscurely carinate, 28–38 mm. long, 18–24 mm. broad, obtuse to truncate at base, rounded and minutely apiculate at apex, densely ferruginous-tomentellous, the pericarp 2–3 mm. thick, the aril copiously laciniate.

Distribution: Fiji, apparently fairly abundant at elevations up to 900 m.

FIJI: *Horne 205* (GH), *243* (GH). VITI LEVU: Tholo North, Nandarivatu, *Gillespie 4312* (NY, US); Namosi, Mount Naitarandamu, *Gillespie 3357* (NY); Naitasiri, Tamavua woods, near Suva, *Gillespie 2032* (NY), *2056* (US). OVALAU: *U. S. Expl. Exped.* (GH—TYPE, NY, US). VANUA LEVU: Mbua, Seatovo Range, *Smith 1537* (GH, NY, US); lower Wainunu River valley, *Smith 1745* (GH, NY, US).

Common names: Male, Male ndina.

The specimens from Vanua Levu have slightly smaller leaves than the others and do not show such a pronounced farinose-ceriferous lower surface of the leaf-blades, but there seems no doubt of their place here. I erroneously mentioned (Bishop Mus. Bull. **141**: 66. 1936) one of these specimens as *M. hypargyraea*, a species not yet known from Fiji.

3. MYRISTICA INUTILIS Rich ex A. Gray, Bot. U. S. Expl. Exped. **1**: 34. 1854; A. DC. in DC. Prodr. **14**: 191. 1856; Warb. Nova Acta Acad. Leop.-Carol. **68**: 481. *pl. 18.* 1897; Guillaumin, Jour. Arnold Arb. **14**: 59. 1933; Christophersen, Bishop Mus. Bull. **128**: 87. 1935; A. C. Smith, Jour. Arnold Arb. **22**: 74. 1941.

Slender tree, up to 20 m. high, the young parts ferruginous-sericeous, the branchlets slender (1–2.5 mm. in diameter distally), subterete, pale brown, at length cinereous, rugose, lenticellate; petioles slender (1–3 mm. in diameter), 10–28 mm. long, pale brown or nigrescent, shallowly canaliculate; leaf-blades papyraceous or chartaceous, oblong- or obovate-elliptic, 12–23 cm. long, 4–8.5 cm. broad, acute to rounded at base, gradually acuminate or cuspidate at apex, glabrous and dark olivaceous above, paler and persistently pale tomentellous beneath, the costa slightly raised above, prominent beneath, the secondary nerves 14–22 per side, erecto-patent, slightly arcuate, obscurely anastomosing, essentially plane or slightly impressed above, prominulous beneath, the veinlets usually obscure; staminate inflorescence axillary or arising from defoliate branchlets, up to 12 mm. long, usually forked near base, rarely simple, the peduncle 1.5–3 mm. in diameter, 1–4 mm. long, the secondary peduncles very short or essentially none, the rachises 2.5–3 mm. in diameter, cicatricose nearly to base, pubescent distally, the bracts ovate, minute, caducous; flowers crowded distally on rachises, pale ferruginous-tomentellous (hairs usually 3–6-branched from base, 0.2–0.4 mm. long, rarely simple), the pedicels slender, up to 4 mm. long, the bracteole submembranous, ovate-deltoid or oblong, obtuse, 1.5–4 mm. long, 1–2 mm. broad; perianth urceolate-cylindric, 4–5 mm. long, 1.5–2.5 mm. in diameter, the lobes 3, deltoid, subacute, 1–1.5 mm. long and broad; androecium 3.5–4.5 mm. long, the stalk slender, 1.5–2 mm. long, faintly stramineous-strigose near base, the anthers 8–11, 1.7–2.5 mm. long, the connective slender, obtuse, usually obviously exceeding the anthers; fruits solitary or paired, usually axillary, the peduncle 4–6 mm. long, 2.5–4 mm. in diameter, swollen distally; fruit oblong-ellipsoid, 23–40 mm. long, 15–23 mm. broad, obtuse at base, obtuse and minutely apiculate at apex, persistently pale tomentellous, the pericarp about 1 mm. thick, the aril finely laciniate, the seed oblong-ellipsoid, up to 32 mm. long and 17 mm. broad.

Distribution: Samoa (and perhaps Tonga) and the New Hebrides, at elevations up to 500 m.; also known from the Solomons.

NEW HEBRIDES—EFATE: Undine Bay, *Kajewski 220* (A). TANNA: Lenakel, *Kajewski 44* (A). ANEITYUM: Anelgauhat Bay, *Kajewski 757* (A). SAMOA: U. S. Expl. Exped. (GH—TYPE, NY, US); *Whitmee* (GH); *Graeffe 79* (GH); *Vaupel 642* (US); *Kuntze 21084* (NY). TAU: near Faleasao, *Garber 609* (NY). TUTUILA: near Pango Pango, *Kuntze 23015* (NY); *Potts 1* (US); above Naval Station, *Christophersen 984* (US), *995* (NY). SAVAII: Salailua, *Christophersen 2612* (US); Tanga, *Christophersen 2338* (NY); near Samalaeulu, *Christophersen 3473* (NY, US). TONGA (?): *U. S. Expl. Exped.* (US).

Common name: Atone, Atoge (in Samoa).

Although one of the Exploring Expedition specimens, as cited, bears the inscription "Tonga," and although the species is mentioned in the original publication as being from "Tutuila, Savaii, and Tongatabu," it may be advisable not to record this species definitely from Tonga until additional and more accurately labeled specimens are available.

The species is a very distinct one and has no close relatives among Pacific species, being apparently of the alliance of the Papuan *M. Buchneriana* Warb. The New Hebrides specimens have the fruits proportionately slightly broader, but this small difference hardly seems to distinguish them specifically from the Samoan specimens. The absence of *M. inutilis* from Fiji is noteworthy and is possibly to be explained by the inadequacy of our material from that group. Christophersen cites several Samoan specimens not available to me, the species being fairly abundant in that group.

4. MYRISTICA CHARTACEA Gillespie, Bishop Mus. Bull. **83**: 5. *f. 2.* 1931; A. C. Smith, Bishop Mus. Bull. **141**: 66. 1936.

Slender tree, up to 15 m. high, the young parts tomentellous, the branchlets subterete, very slender (1–3 mm. in diameter), pale brown, at length cinereous and rugose; petioles slender (1–2 mm. in diameter), 10–26 mm. long, pale brown, shallowly canaliculate; leaf-blades chartaceous, oblong-elliptic, 6–15 cm. long, 2.5–6.5 cm. broad, rounded to acute at base, rounded to obtusely short-acuminate at apex, slightly recurved at margins, olivaceous and concolorous, obscurely and smoothly ceriferous beneath, the costa conspicuously raised above, prominent beneath, the secondary nerves 17–22 per side, erecto-patent, straight, obsoletely anastomosing, essentially plane or faintly impressed above, plane or prominulous beneath, the veinlets obscure, often slightly impressed above; staminate inflorescence axillary or arising from defoliate branchlets, up to 10 mm. long, simple, the peduncle 1–1.5 mm. in diameter, 2–4 mm. long, swollen distally, faintly stramineous-strigose, the bracts broadly ovate, minute; flowers fasciculate at apex of peduncle or crowded on a very short rachis, ferruginous-tomentellous (hairs branched, about 0.3 mm. long), the pedicels up to 1.5 mm. long, the bracteole submembranous, ovate, about 4 mm. long and broad, obtuse; perianth thin-carnose, campanulate, 4.5–5 mm. long, 2.5–3 mm. broad, the lobes 3, deltoid, about 1.5 by 2.5 mm.; androecium stout, carnose, 3.5–4 mm. long, the stalk glabrous, about 1 mm. long, the anthers 6 or 7, 2.5–3 mm. long, free distally and often slightly exceeding the apically convex connective; pistillate inflorescences essentially similar to staminate; perianth urceolate, to 4 mm. in diameter; ovary ovoid, about 2.5 mm. in diameter at anthesis, densely ferruginous-strigose, the stigma deeply cleft; fruits usually solitary, often subsessile, the peduncle up to 10 mm. long and 4 mm. in diameter; fruit ovoid-ellipsoid, 27–50 mm. long, 17–30 mm. in diameter, usually truncate at base, rounded and minutely apiculate at apex, persistently tomentellous, the pericarp rugose, thin (1–2 mm. thick), the aril laciniate into broad lobes, the areoles large, the seed oblong-ellipsoid, up to 40 by 24 mm.

Distribution: Fiji, at elevations between 200 and 900 m.

FIJI: *Seeman 7* (GH). VITI LEVU: *Horne 966* (GH). VANUA LEVU: Thakaundrove, Yanawai River region, Mount Kasi, *Smith 1825* (GH, NY, US); southern slope of Korotini Range, *Smith 501* (GH, NY, US). MOALA: near Naroi, *Smith 1316* (GH, NY, US), *1319* (GH, NY, US).

Common names: Male, Wale.

The type is *Gillespie 4206,* from Nandarivatu, Tholo North, Viti Levu; additional specimens are cited by Gillespie from Namosi and Naitasiri provinces, Viti Levu. The species is readily recognized by its small leaves with inconspicuous nerves and is perhaps most closely related to *M. Gillespieana;* it can be at once distinguished from *M. castaneaefolia* by its lack of the powdery wax characteristic of the under surface of leaf-blades of that species, as well as by obvious floral and other foliage differences.

5. MYRISTICA INSULARIS Kanehira, Fl. Micrones. 115. *f. 35.* 1933; Bot. Mag. Tokyo **47**: 671. 1933.

Tree, up to 10 m. high, the young parts ferruginous-sericeous, soon glabrescent, the branchlets stout (3–5 mm. in diameter distally), rugose, subterete, brown or cinereous; petioles stout (3–4 mm. in diameter), 10–40 mm. long, brownish or nigrescent, conspicuously canaliculate; leaf-blades thin-coriaceous, oblong- to obovate-elliptic, 13–30 cm. long, 5.5–15 cm. broad, rounded to obtuse at base, obtuse at apex, often conspicuously recurved at margins, dark olivaceous above, glaucous and smoothly (rarely inconspicuously farinose-) ceriferous beneath, sometimes sparsely tomentellous beneath when young, soon glabrescent, the costa conspicuously elevated above, prominent beneath, the secondary nerves 16–25 per side, erecto-patent, anastomosing toward margins, usually impressed or occasionally prominulous above, prominent beneath, the veinlets usually impressed above and plane beneath, occasionally faintly prominulous on both sides; staminate inflorescence supra-axillary or arising from defoliate branchlets, 20–40 mm. long, forked, the peduncle 2–3 mm. in diameter, 10–20 mm. long, closely ferruginous-strigose, the secondary peduncles up to 3 mm. long, sometimes essentially none, the rachises, about 3 mm. in diameter, elongate, cicatricose, ferruginous-strigose, the bracts caducous; flowers crowded near apices of rachises, ferruginous-tomentellous (hairs 0.3–0.6 mm. long, several-celled, the lower cells conspicuously transversely fusiform, the apical cell often elongate), the pedicels 2–4 mm. long at anthesis, stout, the bracteole submembranous, broadly ovate to deltoid, 2–3 mm. long, 4–5 mm. broad, obtuse; perianth campanulate, 4–5 mm. long and broad, the lobes 3, deltoid, obtuse, about 1.5 by 3 mm.; androecium stout, 3.5–4.5 mm. long, the stalk 1–1.5 mm. long, sparsely and obscurely stramineous-strigose, the anthers 11–18, 2–3 mm. long, faintly exceeded by the obtuse connective; fruits apparently usually solitary, the peduncle 3–7 mm. long, stout (4–6 mm. in diameter); fruit oblong-ellipsoid, 37–50 mm. long, 23–30 mm. broad, rounded or obtuse at both ends and inaequilaterally apiculate at apex, densely ferruginous-tomentellous, the pericarp brittle, about 1 mm. thick, the aril laciniate into thin lobes, the areoles often large, the seed oblong-ellipsoid, conspicuously marked by the impressions of the aril.

Distribution: Caroline Islands, at elevations up to 300 m.

CAROLINE ISLANDS—TÔDAIYAMA, near Korror: *Kanehira 1865* (NY, type coll.), *2024* (NY, US). BABELDAOB: Galdok, *Kanehira & Hatusima 5009* (NY). PONAPE: *Kanehira 727* (A, NY), *763* (NY), *1512* (NY), *1545* (NY, US).

Common name: Karala (Ponape).

Some of the above-cited specimens have been mentioned by Kanehira (Bot. Mag. Tokyo **45**: 280. 1931; Fl Micrones. 113. *f. 34.* 1933) as *M. hypargyraea,* but I believe them to be all conspecific and to represent an endemic species. *M. insularis* may be separated from its Samoan and Fijian relatives (*M. hypargyraea* and *M. Gillespieana*) by the slight differences in foliage mentioned in my key, and more accurately by the difference in type of pubescence on the staminate inflorescence. This latter character, although it can be observed only with a magnification of 25 times or more, is very constant and is probably the best means of distinguishing *M. insularis.*

6. MYRISTICA HYPARGYRAEA A. Gray, Bot. U. S. Expl. Exped. **1**: 33. 1854; A. DC. in DC. Prodr. **14**: 194. 1856; Warb. Nova Acta Acad. Leop.-Carol. **68**: 479. *pl. 18.* 1879; Christophersen, Bishop Mus. Bull. **128**: 86. 1935.

Tree to 10 m. high or more, the young parts faintly puberulent, soon glabrescent, the branchlets subterete, stout (2–5 mm. in diameter distally), pale brown to cinereous, at length lenticellate and rugose; petioles rugose, 1.5–5 mm. in diameter, 15–35 (–43) mm. long, shallowly canaliculate; leaf-blades thin-coriaceous, oblong or elliptic- or obovate-oblong, 12–35 (–45) cm. long, 4.5–14 cm. broad, rounded to subacute at base, cuspidate or obtuse at apex, slightly recurved at margins, olivaceous and shining above, somewhat glaucous and smoothly ceriferous beneath, the costa sharply raised above, prominent beneath, the secondary nerves 15–25 per side, spreading, straight, ascending and anastomosing toward margins, slightly impressed or faintly elevated above, strongly prominulous or prominent beneath, the veinlets usually obscure, sometimes faintly prominulous or impressed on both surfaces; staminate inflorescences supra-axillary or arising from defoliate branchlets, 10–40 mm. long, forked or occasionally trifid (sometimes simple, at least when young) the peduncle 1.5–3 mm. in diameter, 7–20 mm. long, often persistently strigose, the secondary peduncles up to 5 mm. long, sometimes essentially none, the rachises 3–4 mm. in diameter, cicatricose, puberulent distally, the bracts caducous; flowers crowded distally on rachises, ferruginous-strigose (hairs 0.3–0.7 mm. long, simple or obscurely plumulose near base), the pedicels to 7 mm. long, the bracteole carnose, suborbicular, 3–4 mm. long, 4–5 mm. broad, rounded at apex; perianth carnose, campanulate, at anthesis 5–6 mm. long and broad, the lobes 3, oblong-deltoid, 2.5–3 mm. long, 3–5 mm. broad, obtuse; androecium 2–3.5 mm. long, the stalk stout, glabrous, 0.5–1.3 mm. long, the anthers 7–10, 1.5–2.3 mm. long, faintly exceeding the often apically depressed connective; fruits usually solitary, the peduncle (combined with pedicel) up to 17 mm. long and 4–5 mm. in diameter, often persistently puberulent; fruit broadly ellipsoid or nearly subglobose, 28–40 mm. long, 24–30 mm. broad, rounded at both ends and usually apiculate at apex, persistently strigose or conspicuously tomentellous, the pericarp 1–2 mm. thick, the aril copiously laciniate into narrow lobes, the seed 21–34 mm. long, 18–25 mm. broad.

Distribution: Samoa and Tonga, at elevations up to 700 m.

SAMOA: *U. S. Expl. Exped.* (GH—TYPE, NY, US); *Whitmee* (GH); *Kuntze* (NY); *Horne 10* (GH); *Vaupel 300* (NY). TUTUILA: above Naval Station, *Christophersen 996* (NY). UPOLU: Apolau, *Reinecke 133* (US); above Malololelei, *Christophersen 150* (NY, US), *314* (NY). SAVAII: near Samalaeulu, *Christophersen 3474b* (NY). TONGA—TONGATABU: Mua, *Setchell & Parks 15275* (GH, US). EUA: *Parks 16160* (GH, NY, US).

Common names: Atone, Atone 'ulu (Samoa).

Christophersen has cited several additional Samoan specimens. The original collection is mentioned as from "Tutuila and Savaii" and the species is said to be also from Tongatabu, but I have seen no Exploring Expedition material of the species from Tonga.

7. MYRISTICA GILLESPIEANA A. C. Smith, Bishop Mus. Bull. **141**: 67. *f. 32.* 1936.

Tree to 20 m. high, the young parts soon glabrous, the branchlets terete, 2–4 mm. in diameter distally, brownish, at length cinereous, rugose, and lenticellate; petioles brownish or nigrescent, 2.5–4 mm. in diameter, 10–50 mm. long, shallowly canaliculate; leaf-blades thin-coriaceous, oblong or obovate- or elliptic-oblong, 16–32 cm. long, 5–11 cm. broad, rounded or obtuse or faintly subcordate at base, obtuse or obtusely cuspidate at apex, slightly recurved at margins, olivaceous or dark green above, somewhat glaucous and smoothly ceriferous beneath, the costa slightly elevated to prominent above, prominent beneath, the secondary nerves 18–26 per side, erecto-patent, straight, inconspicuously anastomosing, faintly impressed or essentially plane above, sharply raised beneath, the veinlets often obscure, faintly prominulous or slightly impressed above, immersed or faintly prominulous beneath; staminate inflorescences supra-axillary or arising from defoliate branchlets, (6–) 10–30 mm. long, forked or occasionally trifid, the peduncle 3–4 mm. in diameter, up to 10 mm. long, glabrous, the secondary peduncles up to 8 mm. long, sometimes essentially none, the rachises 3–4 (–5) mm. in diameter, cicatricose, puberulent distally, the bracts broadly ovate, small, caducous; flowers crowded toward apices of rachises, densely ferruginous-tomentellous (hairs branched from or near base, tangled, not exceeding 0.5 mm. in length), the pedicels up to 6 mm. long, the bracteole ovate-deltoid, 3–5 mm. long, 4–6 mm. broad; perianth carnose, subglobose or broadly campanulate, 3.5–6 mm. long and broad, deeply cleft, the lobes 3, deltoid, 1.5–4 mm. long and broad; androecium 2–4 mm. long, the stalk stout, glabrous or obscurely stramineous-strigillose, 0.5–1.3 mm. long, the anthers 8–12, 1.5–2.7 mm. long, slightly exceeding or essentially equalling the obtuse or apically depressed connective; pistillate inflorescence essentially similar, the ovary ovoid, at anthesis about 3 mm. long and in diameter, densely ferruginous-strigose (hairs about 0.5 mm. long), the stigma glabrous, inconspicuously cleft; fruits solitary or paired (peduncle up to 8 mm. long and 10 mm. in diameter, the pedicel also stout, up to 15 mm. long), oblong-ellipsoid, 37–50 mm. long, 23–30 mm. broad, rounded to acute or gradually attenuate at base, rounded to subacute and apiculate at apex, closely ferruginous-tomentellous, the pericarp 1.5–3 mm. thick, the aril finely laciniate, the seed 34–40 mm. long, 20–23 mm. broad.

Distribution: Fiji, at elevations up to 500 m.

FIJI—VITI LEVU: *Seemann 6* (GH). KANDAVU: above Namalata and Ngaloa Bays, *Smith 124* (GH, NY, US). MOTURIKI: *Storck 866* (GH). VANUA LEVU: Mbua, upper Ndama River valley, *Smith 1597* (GH, NY, US). KORO: *Smith 946* (GH, NY—TYPE, US), *1048* (GH, NY, US). MALATTA, south of Vanua Mbalavu: *Smith 1457* (GH, NY, US).

Common name: Male.

In first describing this species, I cited only the type and the Seemann specimen, inadvertently referring the others to *M. castaneaefolia;* subsequent study indicates that the two species are not closely related and that they can be readily distinguished even when sterile by examining the waxy lower surface of leaf-blades. *M. Gillespieana* is less readily separated from the Samoan *M. hypargyraea*, doubtless its closest relative, but the characters of inflorescence-tomentum and fruit-shape mentioned in the key seem sufficiently constant to permit the two species to be retained.

8. **Myristica Guillauminiana** A. C. Smith, sp. nov.

Arbor ad 25 m. alta praeter partes novellas puberulas et fructus glabra, ramulis subteretibus rugosis crassis (apices versus 3–5 mm. diametro) demum conspicue lenticellatis; petiolis rugosis 1.5–2.5 mm. diametro 15–30 mm. longis canaliculatis; laminis chartaceis elliptico- vel obovato-oblongis, 16–24 cm. longis, 5–9.5 cm. latis, basi obtusis et in petiolum inconspicue decurrentibus, apice obtusis vel obtuse cuspidatis, margine paullo undulato-recurvatis, supra olivaceis subnitentibus, plus minusve concoloribus et subtus inconspicue et leviter ceriferis, costa utrinque prominente, nervis secundariis utrinsecus 15–18 erecto-patentibus paullo curvatis inconspicue anastomosantibus supra leviter impressis vel prominulis subtus valde elevatis, venulis inconspicuis supra paullo impressis subtus inconspicue prominulis; fructibus supra-axillaribus vel e ramulis defoliatis orientibus solitariis vel binis, pedunculis crassis (5–6 mm. diametro) brevibus vel subnullis, pedicellis crassis ad 5 mm. longis primo puberulis mox glabris; fructibus subglobosis 27–32 mm. (ad 45 mm. ex Kajewski) diametro manifeste circumcarinatis, utrinque rotundatis et apice conspicue apiculatis, pericarpio tenui ad 1 mm. crasso extra pilis brevibus plumulosis implicatis densissime ferrugineo-tomentello, arillo in lacinias paucas latas fisso, areolis magnis, semine subgloboso.

Distribution: New Hebrides, known only from the type collection.

NEW HEBRIDES—VANUA LAVA, Banks group: *Kajewski 422* (A—TYPE, NY), common in rain-forest near sea-level (large tree 25 m. high; fruit brown, up to 4.5 cm. long and 4 cm. in diameter).

It is a pleasure to name this species in honor of Prof. A. Guillaumin, in recognition of his valuable contributions to our knowledge of the flora of the New Hebrides. The specimen was mentioned by Guillaumin (Jour. Arnold Arb. **13**: 83. 1932) as *Myristica* aff. *Hollrungii* Warb., and indeed this may be its closest relative. *Myristica Hollrungii*, however, in addition to having leaf-blades which are on the average larger and slightly thicker in texture than those of the new species, has fruits which are more elongate in proportion and glabrous at maturity. *Myristica Guillauminiana* is readily separated from *M. Gillespieana* by the proportions of its fruits and from *M. hypargyraea* by its thinner leaf-blades which lack the conspicuous glaucous coat of wax of the Samoan species.

INSUFFICIENTLY KNOWN SPECIES

MYRISTICA GRANDIFOLIA A. DC. in DC. Prodr. **14**: 194. 1856; Seem. Fl. Vit. 205. 1867.

Myristica macrophylla A. Gray, Bot. U. S. Expl. Exped. **1**: 33. 1854; non Roxb. (1832); non Benth. (1853).

Myristica grandifolia is based on a single sterile specimen from Ovalau, Fiji (*U. S. Expl. Exped.*, US, TYPE), which is to be compared with *M. castaneaefolia* and *M. macrantha*. From the first of these it differs by its tremendous leaves, which are reported to attain a length of 2½ feet. Nevertheless, it is entirely possible that leaves from a young shoot of *M. castaneaefolia* are represented; Warburg (Nova Acta Acad. Leop.-Carol. **68**: 494. 1897) has discussed the specimen as a dubious synonym of this species. *M. grandifolia* differs from *M. macrantha* by having its leaf-blades tapering to an acute base, and I doubt if it can be referred to this species. Its true position can be established only by additional field work, which may prove that a third species of this alliance is represented.

MYRISTICA HORNEI Warb. Nova Acta Acad. Leop.-Carol. **68**: 107, nomen. 1897.

This name is merely listed with a question by Warburg and apparently is not again mentioned in his work. It is likely that he had in mind, as the basis of the name, *Horne 966*, which was later (p. 494) briefly characterized as a second species from Fiji (in addition to *M. castaneaefolia*). The Horne specimen is referable to *M. chartacea,* but since Warburg has not definitely tied his name to this specimen, we may certainly continue to use Gillespie's specific epithet and to treat *M. Hornei* as a nomen nudum.

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JAMAICA PLAIN, MASSACHUSETTS

FOREST REPLACEMENT RATES IN THE COLORADO HEADWATERS AREA[1]

RONALD L. IVES

Field studies in the Colorado Headwaters area, largely in Grand County, Colorado, near latitude 40°, between the elevations of 8,000 and 11,000 feet, augmented by studies of numerous photographic collections, including those of the U. S. Geological Survey and of the University of Colorado Museum, supply quantitative data concerning replacement of burned-off evergreen forest in this high-altitude environment.

The normal evergreen forest in parts of this area was burned off during Indian troubles in 1862 and 1863; this created large areas of fire slash, in a few of which even the soil was destroyed down to bedrock.

Photographs taken in 1872 by William H. Jackson, official photographer for the Hayden expedition,[2] show many of the fire-damaged trees dead and barkless, grass growing in the charred soil, and brushy growths springing up in especially favored locations.

Between 1872 and 1887–8, when the next series of clear photographs was taken,[3] many of the fire-killed trees had fallen; aspen, the normal replacement growth, was well established, and in a few places overtopped the dense brush that had grown up since 1872.

Since 1898, the area has been photographed many times.[4] Pictures taken during the decade of 1898–1908 show a rapid crowding out of brushy growths by aspen, which reached its maximum height and density, in normal areas, by about 1915. Small evergreens are detectable in several photographs taken as early as 1900, and by 1920 evergreens just overtopped aspens in many locations.

Many of these old fire scars, in photographs taken about 1920, show an aspen forest containing patches (up to 40 per cent) of evergreen. By 1935 evergreen definitely predominated (60 + %), and by 1940 the forest in these old fire scars was almost entirely evergreen, with aspen present only where evergreen growth was inhibited, as by solifluction or rapid sedimentation.

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[1] Field studies supported in part by grants from the Penrose Fund of the American Philosophical Society.

[2] Many of these photographs, in excellent condition, are in the files of the U. S. Geological Survey. Others are in the Ford Museum, at Dearborn, Michigan. An extensive collection of William H. Jackson's prints is in the Denver (Colo.) Public Library. Additional data may be found in ''Time Exposure,'' by William H. Jackson (Putnam, New York, 1940).

[3] These photographs, in private collections at Grand Lake, are dated, but not signed.

[4] These data are from the Brackett, Henderson, and Tangen photographs, most of which are now in the University of Colorado Museum.

Cuttings from several evergreens in these old fire scars indicate ages exceeding 40 years.

Although areas in which the evergreen forest was destroyed in the 1860's now again contain evergreen forest, they are still easily recognizable, for "replacement" evergreen forest is composed of younger trees than the "residual forest." In consequence, the old scars are visible as areas of definitely smaller trees. Trees in the residual forest have ages up to 350 years, as determined by ring counts.

From these data, the following replacement rates, in terms of years since forest destruction, are indicated for this area:

Maximum brush growth	25	years
Maximum aspen growth	40	years
Aspen largely eliminated	65	years
Complete elimination of scar	300 +	years (estimated)

Where water supply is abnormal, whether too great or too slight, exposure is great, or soil is unstable, rates will be slower. So far as can be determined from this evidence, which is based on foliage area, rather than on "tree counts," transitions from one state to another are rather abrupt, each crowded-out community disappearing rather rapidly once it is overtopped by the next member of the replacement sequence.

Further studies of this type, in areas where old photographs are available, such as those deforested during the Civil War, should produce additional data concerning replacement rates.

Photographs now being taken by the U. S. Forest Service and other organizations should supply much similar data in the future, particularly when the dates and locations are plainly marked on the negatives.

BOULDER, COLORADO

CACTI OF THE CANYON OF THE COLORADO RIVER AND TRIBUTARIES[1]

ELZADA U. CLOVER AND LOIS JOTTER

(WITH EIGHT FIGURES AND A MAP)[2]

The Canyon of the Colorado has been known to geologists since the time of Ives and Powell, but, except for a restricted section included in the Grand Canyon National Park, little or no botanical work has been attempted before the present investigations.

This paper is the result of field studies, the first made during the summer of 1938 on the Nevills Colorado River Expedition. The party traveled in small boats from Greenriver, Utah, to Boulder Dam, Nevada. The manner of travel made it impossible to collect cacti in quantity, since they are bulky whether obtained living or dry. All species observed were collected, some several times, and detailed notes were taken throughout the canyon.

Two stops for supplies were made during the 666 mile journey, at Lee's Ferry and at Grand Canyon. Here plants, which had been carried in closed hatches, were sent back to the University of Michigan Botanical Gardens.

A second expedition was made by the senior author the following summer. This included trips on horseback and on foot down the Kaibab Trail in Grand Canyon to the Colorado; into the Rainbow Bridge area, southern Utah; and Havasupai Canyon, a tributary of the Colorado. The Park Service at Lake Mead made it possible to go to the head of the lake. Collections were made at selected locations from Separation Canyon to Boulder Dam.

Again, it was not possible to repeat collections to any great extent, but accurate information on distribution was obtained. Chiefly phanerogamic flora was studied, and herbarium specimens were collected on both of these expeditions. A complete report, giving an account of the history, geology, and topography of the Colorado River region, and including a list of collected plants, will be published in the near future.

The expedition of 1938 was financed in part by a Rackham Faculty Research Grant and in part by Edgar J. Marston of Colorado Springs, Colorado.

The extremely high, often sheer walls, and the scouring action of the water increase the problems of migration of plants up the floor of the Canyon. The seeds of cacti are not adapted for wind dispersal, so that distribution must be accounted for in other ways. Some species, especially *Opuntia*

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[1] Paper No. 729 from the Department of Botany and the Botanical Gardens, University of Michigan.

[2] Plate 1 is published at the expense of the authors.

acanthocarpa and *O. Bigelovii,* grow high on the walls and may be seen in crevices or pockets in the rock to within 100 or 150 feet of the canyon floor. Joints readily break off and probably fall over the rim, and take root if given an opportunity. Run-off water plays a part in bringing the joints lower in the canyon. None of the *Cylindropuntiae* is found on the lower talus or near the water.

The *Echinocerei,* especially *E. Engelmannii,* are found frequently on low ledges and talus, and some may be seen higher on the walls, showing as they always do a preference for limestone. It is noticeable that the caespitose forms have fewer stems than those up on the desert. The extreme heat on the rock walls and a lack of soil may cause sparsity of growth. Many plants have great difficulty in surviving these extreme conditions. This is evidenced by withered and dying cacti on dry ledges. It is interesting to note that the same species may also languish among boulders on deltas and sandy shores. Here is a case where drought vies with flood waters in exterminating plants struggling for existence in a trying situation. Flood waters bring plants down side canyons and farther into the gorge of the Colorado where they lodge between boulders and, often half-buried, take root. *Opuntia basilaris* and others belonging to this series are the only species found near the water's edge. In normal desert habitats they may be found both at high and low altitudes and in the shade of shrubs and trees, as well as among the rocks in the hottest possible places on the desert. The growth in canyons is much less luxuriant, consisting often of only two or three joints. This may be accounted for to some extent by the fact that stems are torn apart by floods or by landslides. These joints take root and barely become established before they are again uprooted.

In contrast, a permanent delta at Nankoweap Rapids (above Bright Angel Creek) supports an abundant and vigorous association of *Opuntia polyacantha, O. hystricina, O. phaeacantha,* and *Echinocereus Engelmannii* (fig. 1). These, with mesquite and *Acacia,* form a typical desert scrub covering. The many boulders strewn over this area afford protection to plants until they gain sufficient foothold to withstand the wash of flood waters, which in so wide a space cannot be deep and swift.

Certain sections in Havasupai Canyon are particularly favorable to the growth of certain cacti. Supai shale is very productive, and in places *Opuntiae* flourish almost to the exclusion of other plants.

The flora of the canyons studied is typical of the Sonoran zone, as defined by Merriam. An arm of the Upper Sonoran extends north from Lee's Ferry along the Colorado River and for some distance up such tributaries as the San Juan River and Forbidding Canyon. *Atriplex canescens* and *Salix exigua* are typical Upper Sonoran species and cacti associated with them include *Opuntia polyacantha* and *Echinocereus octacanthus.*

At Lee's Ferry the Colorado flows southwest into deeper canyons where the inner and warmer portions of the gorge support a Lower Sonoran flora. Prominent in the vegetation of this area are mesquite, *Acacia*, and creosote bush. Although the last species is recognized as typically Lower Sonoran, it is not common above Lava Falls. Creosote bush (*Larrea*) apparently requires a higher temperature than those species found in the northern reaches of this zone. *Ferocactus acanthodes* (fig. 3) and *Phellosperma tetrancistra* are commonly found in the Lower Sonoran, and the latter occurs northward as far as Rainbow Bridge.

When a southern species is reported over two hundred miles beyond the northern limits of its range, it is possible that a thorough search on the desert would show a more or less continuous distribution.

Conditions seem to be unfavorable for the *Coryphanthae* although members of this genus are abundant in other parts of the Lower Sonoran. Most western species require a relatively high altitude, which may account for their complete absence here.

Echinocactus polycephalus Engelm. & Bigelow. Usually in clumps of from several to many rounded heads. Occasional on the Bright Angel shale in Spencer (*4446*) and Separation Canyons. Undoubtedly scattered on walls of Lake Mead to some distance below Pierce Ferry (*4447*) where it is found infrequently. Commonly associated with *Ferocactus acanthodes* but not extending so far north. (Fig. 2.)

Distribution: Southern Nevada, California, possibly in extreme southern Utah, western Arizona, northern Sonora and reported from Lower California.

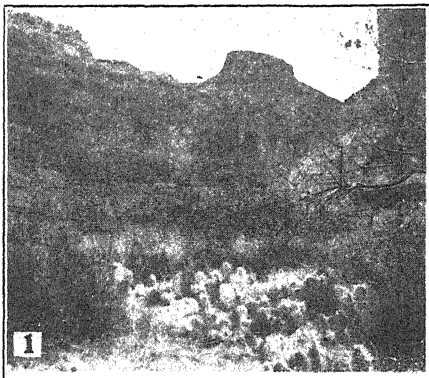
Echinocereus acifer (Otto) Lemaire? Caespitose, sometimes solitary, erect, stem bright green, spines brown. There is a possibility that this is a new species. It fits the description of *E. acifer* very well (flowers have not been observed), but is entirely out of the reported range. Fairly common on limestone ledges above the river in Narrow Canyon near the mouth of the Dirty Devil River (*2184*).

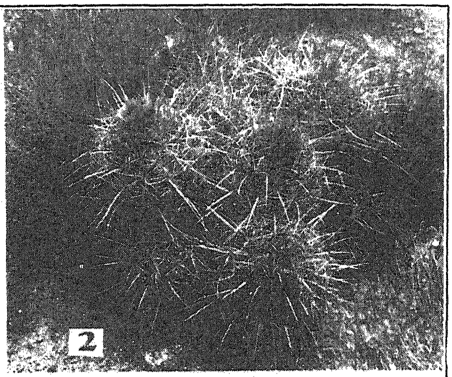
Distribution: Durango and Coahuila, Mexico; Narrow Canyon, Canyon of the Colorado, San Juan Co., Utah.

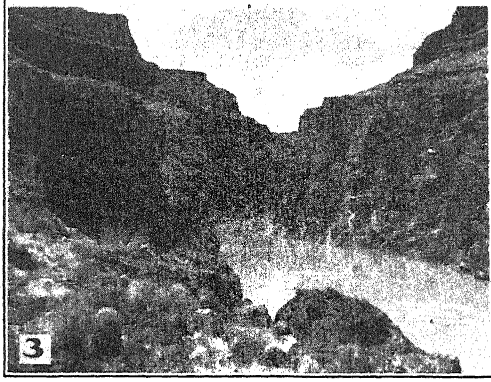
Echinocereus octacanthus (Mühlenpfordt) Britt. & Rose. Growing on limestone ledges. Mouth of the Dirty Devil River (*2184A*); Surprise Valley; Rainbow Bridge; Vasey's Paradise; above Bright Angel in Grand Canyon; Hermit Creek (*2303*); two miles above Bass Cable (*2317A*); and Elves' Chasm. This represents a considerable extension of range.

Distribution: Northwestern Texas; and reported from New Mexico and Utah.

Echinocereus coccineus Engelm. This species is often confused with *E.*







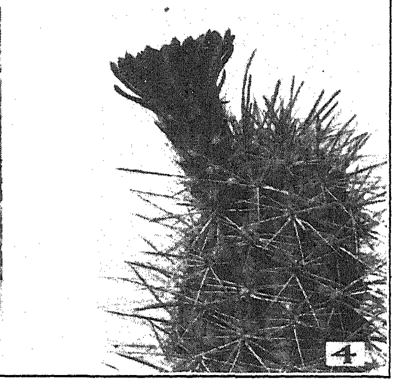


FIG. 1. Well-established association including *Opuntia polyacantha*, *Echinocereus Engelmannii*, and *Acacia Greggii* growing on the right of the Colorado at Nankoweap Rapids. FIG. 2. *Echinocactus polycephalus;* occasional on steep talus in Lower Grand Canyon. FIG. 3. Habitat of *Ferocactus acanthodes* near Separation Canyon; common throughout the Lower Sonoran within the Canyon of the Colorado and tributaries. FIG. 4. *Echinocereus canyonensis;* occasional at Bass Cable on a limestone outcrop.

octacanthus although they are very distinct. Occasional from Narrow Canyon (*2186*) to Lake Mead.

Distribution: New Mexico and Arizona to Utah and Colorado.

Echinocereus Engelmannii (Parry) Rümpler. More abundant in the Canyon than any other species. It appears well able to adapt itself to difficult situations. Often found clinging to rock ledges hundreds of feet above the floor of the Canyon, probably started from seeds which fell over the rim. This species is also found on steep talus slopes, on limestone ledges above the river, and on boulder-strewn deltas of side canyons. Collections and plants noted at the following locations: Mormon Trail in Glen Canyon; in the canyon of the San Juan River; Rainbow Bridge; Lee's Ferry; President Harding Rapids; Havasupai Canyon (*4334*); Nankoweap Rapids; 205 Mile Canyon; Spring Canyon; Diamond Creek; Separation Canyon; Spencer Canyon; Quartermaster Canyon; Boulder Dam. (Map, plate 1.)

Distribution: California, Nevada, Arizona, Utah, northern Mexico and Lower California.

Echinocereus Fendleri (Engelm.) Rümpler. This is a variable species with spines ranging from ¼ inch to 3 inches in length. Only the long-spined form was found in the Colorado River region. It was first seen in Marble Canyon on an extensive talus at President Harding Rapids (*2281*); Saddle Canyon; Granite Rapids; Elves' Chasm; Havasupai Canyon; usually associated with *E. Engelmannii*, never abundant.

Distribution: Texas, Utah, Arizona, Sonora, and Chihuahua.

Echinocereus mojavensis (Engelm. & Bigelow) Britt. & Rose. Occasional on talus and limestone or sandstone ledges. Hell Roaring Canyon (*2112*); Dark Canyon; President Harding Rapids; Vasey's Paradise; Spencer Canyon; Separation Canyon.

Distribution: Southeastern California, Nevada, Utah, western Arizona.

Ferocactus acanthodes (Lemaire) Britt. & Rose. First seen 26½ miles below Lee's Ferry (*2239*); Vasey's Paradise on talus (*2271*); Mile 39 below Lee's Ferry; President Harding Rapids (*2272*); Saddle Canyon; Granite Rapids; Bass Cable; Elves' Chasm; common at Conquistadore Aisle and in Havasupai Canyon; very common at Lava Falls (*2371*); Separation Rapids; Spencer Canyon (*4263A*); Emery Falls (*4254*). These plants are usually found on steep talus slopes, apparently coming into the canyon over the top, judging from their occurrence high on the walls. As the water rose in Lake Mead many of these large plants were submerged, and may be seen floating in the water; others are entirely covered except for an inch or two of bristling spines. (Map, plate 1.)

Distribution: Southeastern California, northern Lower California, southern Nevada, southern Utah and northern Arizona.

Opuntia Whipplei Engelm. & Bigelow. Never abundant but occurring on upper talus and on ledges. Vasey's Paradise on steep talus near gushing spring; Upset Rapids; two large clumps found on talus near Walthenburg Rapids; Diamond Creek on ledges; 192 Mile Rapids; Havasupai Canyon (*Gard. 17165*[2]). Found down Hualapai Canyon to Havasupai and on to the Colorado.

Distribution: Northern New Mexico and Arizona, southwestern Colorado, and southern Utah.

Opuntia tetracantha Toumey. Single specimen found growing in sand about two hundred yards up Diamond Creek (*2402*). It is difficult to explain its presence here, since the reported range is only in the vicinity of Tucson, Arizona.

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[2] Here and in following paragraphs this abbreviation refers to the number assigned to a plant in the University of Michigan Botanical Gardens.

Opuntia acanthocarpa Engelm. On high ledges and talus from Havasupai Canyon to Boulder Dam. Boulder Dock (*4180*); 217 Mile Canyon; Diamond Creek (*2396*); Quartermaster Canyon (*4277*).

Distribution: Southern Utah, Arizona, California. Reported from Sonora.

Opuntia echinocarpa Engelm. & Bigelow. Fairly common on steep talus and rock ledges, Spencer Canyon (*4450*).

Distribution: Nevada, Utah, Arizona, California, and Lower California.

Opuntia Bigelovii Engelm. Found from 205 Mile Canyon (below Lava Falls) to Spencer Canyon. This stretch is considerably south of any other part of the river. 205 Mile Canyon (*2388*); Diamond Creek; Quartermaster Canyon; Spencer Canyon.

Distribution: Central and southern Arizona and California, northern Lower California and northern Sonora.

Opuntia molesta Brandegee. Diamond Creek (*Gard. 16850*). This is an extension of the range, which may be accounted for by the fact that the genus Opuntia is not well understood and that the area is not well collected.

Distribution: Heretofore reported only from Lower California.

Members of the series Basilares occur at intervals from Cataract Canyon just below the confluence of the Green and the Colorado Rivers to Boulder Dam. Most of those in the upper Canyon are small and variable. Their existence seems to be precarious since they are usually found half-buried in sand or lodged between boulders. Occasional plants may be found at the base of the steep talus a short distance above the river.

Opuntia basilaris Engelm. & Bigelow. Usually rare, and high up on ledges. Mile 26½ in Marble Canyon; abundant near Vasey's Paradise; Mile 39 below Lee's Ferry; Diamond Creek; Spencer Canyon (*4440*); Separation Rapids; Boulder Dam.

Distribution: Northern Sonora, western Arizona, southern California, Nevada, and Utah.

Opuntia basilaris Engelm. var. This plant differs from *O. basilaris* in having smaller, narrow joints branching from the base, and extremely small areoles. It answers the description of the horticultural variety *nana*, as given by Borg. Spencer Canyon (*4248*).

Opuntia brachyclada Griffiths. Small and caespitose, this species does not produce the broad clumps in the canyon which it does in southern Utah. Mile Rapids, Cataract Canyon (*2111*); and Forbidding Canyon (*2404*), Utah.

Distribution: Southern Utah, and Mescal Canyon, San Gabriel Mts., California.

Opuntia aurea Baxter. Although this is considerably out of the range and habitat as described by Baxter, the plant appears to belong here. Indian Gardens, Grand Canyon, Arizona (*4165*).

Distribution: Both sides of the Arizona-Utah line near the Kaibab Indian Reservation and west to the lower slopes of the Sierras, near Bishop, California; south to near Silver Lake, San Bernardino Co., California. Reported also from Cane Beds, Pipe Springs; between Zion Park and Mt. Carmel; and south on the road to Kanab, Utah.

Opuntia Vaseyi (Coulter) Britt. & Rose. Several spreading plants growing on a limestone outcrop two miles above Bass Cable (*2318*). This is another species with a peculiar distribution. Hitherto it has been reported only from San Bernardino, San Diego and Orange Counties, California.

Opuntia phaeacantha Engelm. Variable species found occasionally in Marble Canyon and Grand Canyon. Vasey's Paradise on dry talus near gushing spring (*Gard. 16871*); Nankoweap Rapids (*2273*); President Harding Rapids; and Indian Gardens on the Bright Angel Trail (*4167*).

Distribution: West Texas to New Mexico, Arizona and northern Mexico.

Opuntia Engelmannii Salm-Dyck. A large species with a more southern range than many of this genus; found usually in undisturbed areas where typical desert vegetation is well established. Two miles above Bass Cable (*2316*); listed at President Harding Rapids; Kwagunt Rapids; below Saddle Canyon; very abundant at Granite Rapids; Elves' Chasm; Havasupai Canyon.

Distribution: Texas, New Mexico, Arizona, Durango, Chihuahua, and Sonora.

Opuntia mojavensis Engelm. Rather common in Havasupai Canyon on top of the red wall limestone below the Bright Angel Shale; common on the flat above Bridal Veil Falls (*4438; Gard. 17169*). Hitherto reported from southern California, southern Utah, and western Arizona.

Opuntia laevis Coulter. Below Granite Rapids (left bank) among boulders (*Gard. 16851*).

Distribution: Southern Arizona, abundant in the mountains about Tucson.

Opuntia chlorotica Engelm. & Bigelow. Occasional near Lee's Ferry (*4335*); Nankoweap Rapids; two miles above Bass Cable (*2316*); Havasupai Canyon (*4441*).

Distribution: Both sides of the Colorado from the San Francisco Mts. to the headwaters of the Williams River and to Mojave Creek, Arizona; southern Utah, New Mexico to Nevada, California, Lower California, and Sonora.

Opuntia erinacea Engelm. An attractive species conspicuous for long, white, often hair-like spines; found commonly from lower Glen Canyon to upper Lake Mead. Forbidding Canyon (*2404*); Nankoweap Rapids on the very dry areas away from the river; Havasupai Canyon (*4434*) on Supai formation above Bridal Veil Falls; listed at Bass Cable and Separation Rapids.

Distribution: Northwestern Arizona, southern Utah, southwestern Colorado, southern Nevada, and eastern California.

Opuntia hystricina Engelm. & Bigelow. A doubtful specimen was found at Hell Roaring Canyon, growing with *O. rhodantha.* These two species somewhat resemble each other and the collected specimen may be an unusual form of *O. rhodantha* (*2081*); Forbidding Canyon on sand "hills" and ledges (*2401*). A robust form was found at Lee's Ferry on a rocky hillside near the Colorado. The joints were ¾ inch thick with reflexed flattened strong spines (*4333*). E. W. Nelson first reported a form collected here in 1909. Also seen at Saddle Canyon; Nankoweap Rapids; and Havasupai Canyon.

Distribution: New Mexico, Arizona, and Nevada.

Opuntia rhodantha Schumann. This species is fairly common along the Green River and the upper Colorado. Hell Roaring Canyon (*2078, 2079, 2082, 2100*); Lee's Ferry, on rocky hillside near the Colorado (*4300*).

Distribution: Northern Arizona, Utah, Colorado, western Nebraska.

Opuntia polyacantha Haworth. A widespread species of varying forms. Near Greenriver, Utah (*1990, 2016,* the latter a red-flowered form); Mile 84 on the Green River; abundant at Hell Roaring Canyon; Cataract Canyon; Forbidding Canyon; Lee's Ferry, Tanner Rapids; in Grand Canyon at President Harding, Nankoweap, and Kwagunt Rapids; Hermit Creek; Granite Rapids. (Map, plate 1.)

Distribution: North Dakota to Nebraska, northwest Oklahoma, west Texas, Arizona, Utah, Washington, and Alberta.

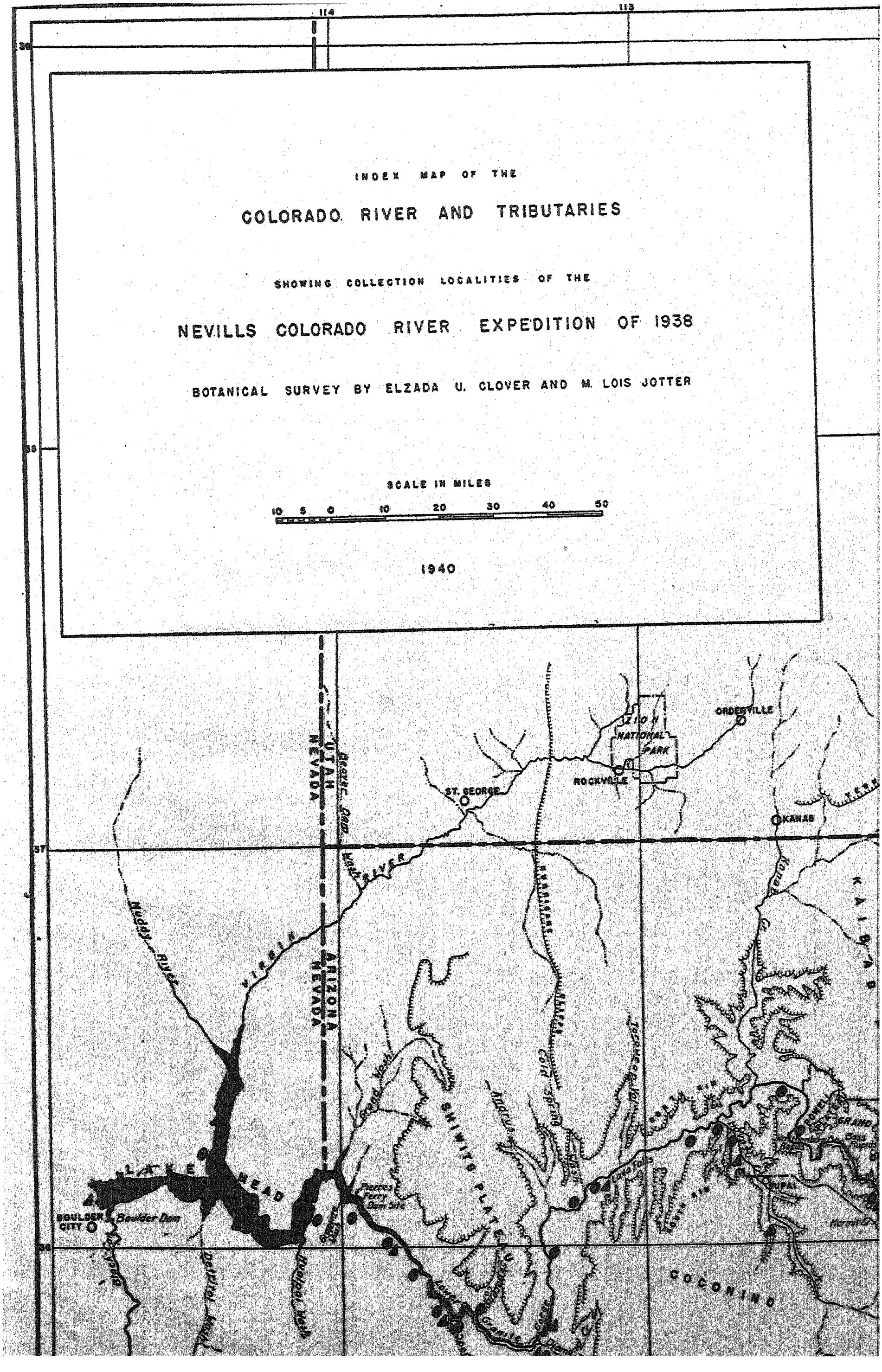
Phellosperma tetrancistra (Engelm.) Britt. & Rose. This genus appears first at the mouth of Forbidding Canyon, near Rainbow Bridge; Mile 26½ in Marble Canyon (*2240*); Vasey's Paradise; Saddle Canyon; Granite Rapids; Bass Cable; Elves' Chasm; Havasupai Canyon (*4442*); Diamond Creek; Separation Canyon (*4247*); Spencer Canyon; Emery Falls (*4287*).

Distribution: Western Arizona, southeastern California, southern Utah, southern Nevada and probably northern Lower California.

Sclerocactus Whipplei (Engelm. & Bigelow) Britt. & Rose. On the Green River at Mile 84; Hell Roaring Canyon.

Distribution: Southeastern Utah and western Colorado.

Sclerocactus polyancistrus (Engelm.) Britt. & Rose. Below Mile Rapid (*2113*) on hot canyon wall. The fruits of this specimen were pink instead of magenta as described.



INDEX MAP OF THE

COLORADO RIVER AND TRIBUTARIES

SHOWING COLLECTION LOCALITIES OF THE

NEVILLS COLORADO RIVER EXPEDITION OF 1938

BOTANICAL SURVEY BY ELZADA U. CLOVER AND M. LOIS JOTTER

SCALE IN MILES

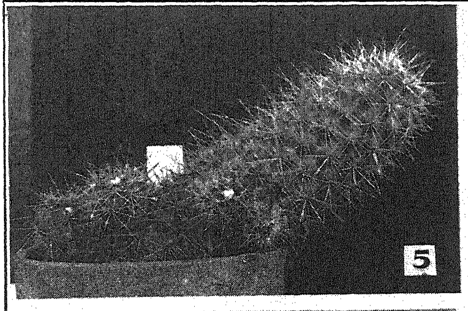
1940

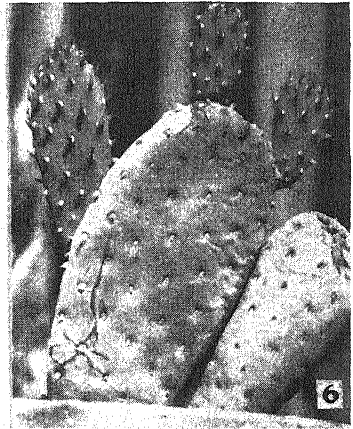
Echinocereus decumbens Clover and Jotter, sp. nov. Cylindricus simplex, decumbens, ramis lateralibus recte divergentibus; costis 10, prominentibus, luteo-viridibus, subcrenatis; areoleis 1–1.3 cm. inter se distantibus, rotundis; spinis lateralibus radiatis 11–12, acicularibus, inequalibus, superioribus quam inferioribus brevioribus 5–10 mm. longis, porrectis albis, apice fuscis; centralibus 2–3, basi bulbosis, subcompressis; 2 summis 1–1.5 cm. longis, ascendentibus; 1 inferiore, 2–3 cm. longa, decurvata. TYPUS (*Clover et Jotter 2212*) vivus ex loco dicto "Marble Canyon"; flum. Coloradensi, conservatus est in Horto Botanico Universitatis Michiganensis.

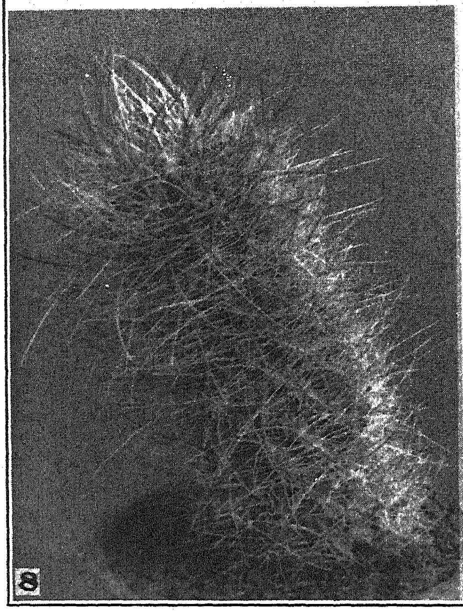
Decumbent, branching at right angles; ribs 10, yellowish-green, prominent, tubercles not prominent; areoles 1–1.3 cm. apart, circular, filled with tawny wool when young, naked in age. Radial spines 11–12, unequal, shorter in upper part of areole, 5–10 mm. long, spreading, white, tipped with red-brown, acicular; centrals 2–3, somewhat flexible, bulbous at the base, slightly flattened, red-brown when young, rose-color to whitish in age. Two upper centrals pointing up and outward, 1–1½ cm. long, lower central strongly deflexed, 2–3 cm. long; TYPE on limestone ledge 30 feet from the river's edge and at the base of a rocky talus at Mile 16½, Marble Canyon, Coconino Co., Arizona (*Clover and Jotter 2212*). Living specimen at the Botanical Gardens of the University of Michigan, Ann Arbor, Michigan (*Gard. 16870.* Fig. 7).

Echinocereus canyonensis Clover and Jotter, sp. nov. Caespitosus, 15–20 cm. altus, 4.5–5 cm. crassus, costis 12–13, cyanei-viridibus, obtusis; areolis rotundis, remotis, inter se 1.5 cm. distantibus, juventate fulvis, tomentosis, aetate nudis; spinis 10–12 lateralibus radiatis, acicularibus, 5 mm.–2.5 cm. longis, rigidis; centralibus plerumque 4, basi bulbosis, fuscis vel nigris, angularibus vel compressis, luteis, saepe maculis purpureo-bruneis variegatis; spinis vetustioribus cinereo-roseis vel purpureo-roseis, porrectis, inferioribus uncinatis, 2.5 vel plerumque 4.5 cm. longis, superioribus 1.5–2.5 cm. longis; floribus in summitate solitariis, parvis sanguineis, 5 cm. longis, 4.3–4.5 cm. crassis; bracteis rubris 2 mm. longis; areolis albis, lanatis; spinis quam 1 cm. brevioribus, apice roseis; segmentis biseriatis, angustis, viridescentibus basi, 5 mm. crassis, apiculatis; stylo viridescenti, stigmatis lobis viridibus 8, plerumque 6 mm. longis; filamentis viridibus vel sursum rubri-purpureis; antheris rubri-purpureis; fructibus ignotis. TYPUS (*Clover et Jotter 2317*) vivus ex loco dicto "Hermit Creek," flum. Coloradensi, Coconino Co., Arizona, conservatus est in Horto Botanico Universitatis Michiganensis, Ann Arbor, Michigan.

Caespitose, 12–15 stems, 15–20 cm. tall, 5 cm. across, blue-green, ribs 12–13, obtuse; areoles remote, 1.5 cm. apart, circular, filled with tawny wool when young, naked in age; radial spines 10–12, acicular, somewhat flattened, yellowish when young, darker at tips, becoming dirty white to purplish in age, pectinate to spreading, irregular in length, 5 mm.–2.5 cm. long (commonly 1.5 cm.), rigid; centrals mostly 4, darker and stronger than the radials, bulbose at the base, angled below and flattened toward the tip, young spines yellowish, mottled with dark brown above, light beneath, porrect, lower one somewhat deflexed, upper centrals 1.5–2.5 cm. long, lower one 2.5–4.5 cm. long. Flower buds appearing at upper part of areole, flowering February 22 and remaining open five days; flowers 5 cm. long, 4.3–4.5 cm. across, areoles on ovary about 1 cm. apart, bracts reddish, 2 mm. long, areoles white wooly, spines short to 1 cm. long, white, sometimes pink-tipped; petal-like part of perianth in two whorls, segments very narrow, greenish at the base, scarlet







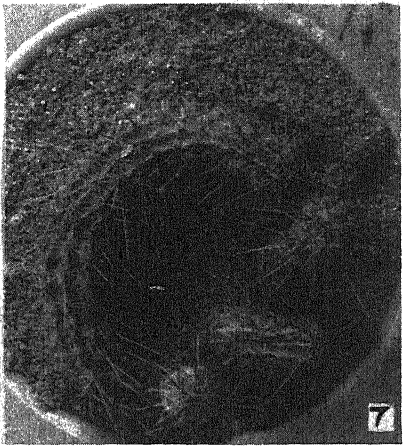


FIG. 5. *Echinocereus canyonensis.* FIG. 6. *Opuntia longiareolata;* rare on steep talus, Granite Rapids. FIG. 7. *Echinocereus decumbens;* single specimen, very different in habit from any other *Echinocereus* in the Canyon. FIG. 8. *Sclerocactus parviflorus;* abundant in lower San Juan Canyon and in restricted areas in Glen Canyon.

toward the tip, apiculate; style greenish, stigma lobes 8, bright green, 6 mm. long; stamens reaching to base of stigma lobes, filaments green below, reddish-purple above, anthers reddish-purple. TYPE (*Clover and Jotter 2317*) collected in a sandy pocket on a steep limestone outcrop 100 yards from the river, Bass Cable below Hermit Creek Rapids, Grand Canyon, Coconino Co., Arizona. Locally abundant. Living specimen in the Botanical Gardens (*Gard. 16846*), University of Michigan, Ann Arbor, Michigan. (Figs. 4, 5.)

Opuntia longiareolata Clover and Jotter, sp. nov. Humilis, articulis spathulatis, glaucescentibus, pubescentibus, adscendentibus e basi proliferis; foliis subulatis minutis, depressis, viridi-rubellis, curvatis; areolis subconfertis, depressis albo-tomentosis, setis numerosis brevibus, roseis vel stramineis, lana circumdatis, demum nudatis; floribus ignotis. TYPUS (*Clover et*

Jotter 2302) vivus ex loco "Granite Rapids," flum. Coloradensi, Coconino Co., Arizona, dicto conservatus est in Horto Botanico (*Gard. 16852*) Universitatis Michiganensis.

Plant belonging to the Series Basilares; joints few, branching from the base and also from top and sides of joints; joints tomentose, elongated, 10–12 cm. long and 4.5 cm. across, spathulate; areoles 8–10 mm. apart, circular on very young joints, these filled with white wool entirely surrounding the pinkish to straw-colored glochids which are early-deciduous, areoles very soon becoming much elongated, 3 mm. long and 1 mm. wide; leaves 4 mm. long, green with burgundy tip, curved, awl-shaped; old joints becoming pale yellow-green in contrast to the deep blue-green of young ones. TYPE (*Clover and Jotter 2302*) growing at base of steep talus, near water's edge, Granite Rapids (*Gard. 16852*), Grand Canyon, Coconino Co., Arizona. (Fig. 6.)

Sclerocactus parviflorus Clover and Jotter, sp. nov. Simplex cylindricus erectus, vel curvatus, 1–4.5 dm. altus, 6–9 cm. crassus; areolis orbiculatis; costis 13, tuberculis prominentibus; spinis 14–15 lateralibus, radiatis, compressis, superioribus quam inferioribus brevioribus, 3.4 cm. longis, apice adustis; spinis centralibus 3 angulatis, summa singula triquetra, alba apice adusta, plerumque curvata, flexuosa, 5–6 cm. longa, ascendenti; inferioribus triquetris vel quadrangulatis, purpureofuscis, 6–7.5 cm. longis, uncinatis, decurvatis; lateralibus 2 purpureo-fuscis, 5.5–6 cm. longis, porrectis; floribus in axillis summis solitariis, parvis, 2.5 cm. longis, 2 cm. crassis, exterioribus in media parte atropurpureis, marginibus et apice scariosis; interioribus purpureis, segmentis crassis, 2-seriatis, apice acuminatis, erosis; stylo purpureo-rubro, stigmatis lobis 10, filamentis viridibus, numerosis, delicatis, antheris luteiaurantiacis, quam stylo brevioribus; fructibus siccis. TYPUS (*Clover et Jotter 2398*) vivus ex "Forbidding Canyon," flum. Coloradensi, Coconino Co., Arizona, dicto conservatus est in Horto Botanico (*Gard. 16845*) Universitatis Michiganensis, Ann Arbor, Michigan.

Plants solitary, oblong, tapering slightly toward the tip, 1–4.5 dm. high; ribs 13, strongly tuberculate; areoles 1.5 cm. apart, sub-circular, plant entirely covered by a dense mass of long, curved and twisting spines; radials 14–15, white with dark tips, much flattened, heavier and longer, 3.4 cm. in the lower part of the areole, central spines 4, the upper one white to horn-colored, tipped with red-brown, 3 angled, flexible, 5–6 cm. long, pointing upward, the lower central 3–4 angled, 6–7.5 cm. long, pointing downward, the two lateral centrals 5.5–6 cm. long, slightly ascending; all centrals except uppermost reddish and curved or hooked. Flowered April 17, remaining open for three days; bud conic, brownish; flower 2.5 cm. long, 2 cm. across; outer perianth segments phlox-purple, in 2 whorls of 8 segments each; these broad with erose margins, acuminate, tube scarcely present; style purplish, stout, longer than the stamens, stigma lobes 10, flattened below, curving outward, 1.5–2 mm. long, amaranth purple; stamens bright orange-yellow, filaments green, very delicate; fruit unknown. TYPE collected at the mouth of Forbidding Canyon in Glen Canyon above Lee's Ferry, Canyon of the Colorado. Abundant 20 miles above Moki Creek, and fairly common at intervals along the lower San Juan River (plate 1). Living specimen (*Clover and Jotter 2398*) at the Botanical Gardens (*Gard. 16844*), University of Michigan, Ann Arbor, Michigan. (Fig. 8.)

UNIVERSITY OF MICHIGAN
ANN ARBOR, MICHIGAN

INDEX TO AMERICAN BOTANICAL LITERATURE

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

Papers that relate exclusively to bacteriology, forestry, agriculture, horticulture, manufactured products of vegetable origin, or laboratory methods are not included. If users of the Index will call the attention of the editor to errors or omissions, their kindness will be appreciated.

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A CYTOLOGICAL STUDY OF CARTERIA CRUCIFERA[1]

VIRGINIA AKINS

(WITH THIRTY-NINE FIGURES)

The genus *Carteria* was named by Diesing (1866), whose type species was *C. cordiformis,* previously described by Carter (1858) as *Cryptoglena cordiformis.* The original description of the species used in this study, *Carteria crucifera* Korshikov, is apparently that given by Pascher (1927), since no description by Korshikov has been found prior to that included in his "Volvocineae" (1938). It is probable that Pascher obtained the description from Korshikov by private communication.

Kofoid and his students have shown that centrosomes and a neuromotor apparatus occur in many animal-like flagellates. Reports of similar structures in the plant-like flagellates have been viewed with skepticism by phycologists because of the incomplete and contradictory evidence. *C. crucifera* was selected for study for two reasons. First, it had been suggested that there might be a correlation between the double number of flagella in *Carteria* and the number of chromosomes. Since the chromosome number had been reported for several species of *Chlamydomonas,* there was a basis for an approximate comparison. Secondly, the position of the pyrenoid anterior to the nucleus reduces the danger of mistaking the narrow layer of cytoplasm between the contractile vacuoles for a rhizoplast.

MATERIALS AND METHODS

The strain of *Carteria crucifera* used for this study was isolated in 1927 by Dr. R. I. Evans from a sample collected in Durham, N. C., and has since

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[1] The writer wishes to express her appreciation to Dr. C. E. Allen for his advice and encouragement during the course of this study, which was carried out under his direction in the Department of Botany of the University of Wisconsin; to Dr. R. I. Evans, Department of Botany, University of Wisconsin, who supplied the culture used; to Dr. L. E. Noland, Department of Zoology, University of Wisconsin, for his helpful suggestions; to Dr. T. E. Hazen and Dr. H. C. Bold, Department of Botany, Barnard College, Columbia University, who identified the species used; and to Dr. J. McA. Kater, Department of Biology, Fordham University, who kindly sent some of his preparations for comparison. The work was carried out with the aid of a University Scholarship and of a grant from the Wisconsin Alumni Research Foundation.

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been kept in culture on nutrient agar[2] at the University of Wisconsin. Stock cultures grew most satisfactorily when kept at about 18° C. under constant illumination. Rapidly growing motile cells were obtained by transferring portions of the agar cultures to low bulb pots filled with quartz sand which were placed in pot-saucers containing a solution composed of about 300 cc. of distilled water to 15 cc. each of Knop's solutions A and B. The cultures were almost entirely covered with glass plates and kept in the greenhouse at 60–65° F.

Nuclear division figures were most abundant in cultures which had been growing on sand for 5–10 days. Counts made at 7 a.m. and 7 p.m. for several periods of three weeks each showed no appreciably greater increase in the number of cells during the night than during daytime. Evidently under cultural conditions cell division is not limited to periods of darkness.

Material to be fixed was centrifuged, mixed with fresh egg albumen, and then smeared on slides and cover glasses which were dropped face down into the fixative. Some of the centrifuged material was placed in vials, fixed, and imbedded in paraffin. To prevent loss of the material, the paraffin was allowed to harden in the narrow vials, and after it was cold the vials were broken. Sections were cut 2–3 μ thick. Schaudinn's alcohol-sublimate solution, with or without acetic acid, used either hot or cold, was the most satisfactory fixative. Carnoy's alcohol-acetic solution, Flemming's medium solution and Randolph's and Belling's modifications of Navashin's fixative also gave satisfactory results.

Some of the preparations were stained with Heidenhain's iron-alum haematoxylin and counterstained with 0.1 per cent Bordeaux red. This method brought out the nucleus, pyrenoid, and the structure of the cytoplasm. Feulgen's nucleal reaction (Robertson 1927) counterstained with fast green proved the most satisfactory method for demonstrating nuclear structure, since neither the nucleolus nor any cytoplasmic structures were stained. Ehrlich's haematoxylin was satisfactory for both nuclear and cytoplasmic structures. Flemming's triple stain was used to study the chloroplast in sectioned material, and F. H. Smith's (1934) modification of the crystal violet-iodine stain was helpful in observing starch formation. Living cells were treated with an aqueous solution of iodine (0.15 per cent) in potassium iodide (0.3 per cent) to identify starch.

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[2] To one liter of 1.4% plain agar the following salts were added:

Potassium nitrate	1.0	gram
Calcium sulphate	0.5	"
Magnesium sulphate	0.5	"
Ferrous phosphate	0.25	"
Tribasic calcium phosphate	0.25	"

Eight-ounce screw-cap bottles, each containing about 60 cc. of the agar, were sterilized and slanted.

OBSERVATIONS

The living motile cells of *C. crucifera* are ellipsoidal and slightly asymmetrical, one side often appearing more convex than the other in optical section (fig. 1). The cells range from 15 to 22 μ in length and from 7 to 14 μ in width. The size varies with cultural conditions and with different stages of growth. The wall (pellicle) is distinct and is thickened anteriorly to form a relatively large papilla. In a surface view looking toward the anterior end of the cell this protuberance presents somewhat the shape of a cross, and the four flagella project from the cell through fine canals, one in each of the depressions between the arms of the cross. The light green chloroplast appears to fill the cell except for a small concave region in the anterior end. Occasionally there is a small irregular clear region at the posterior end. In surface view longitudinal striations of the chloroplast are visible. A small ovoid red pigment-spot is located either in the outer layer of the chloroplast or between the wall and the chloroplast in the anterior half of the cell (fig. 1).

The pyrenoid occupies the greater portion of the middle part of the cell and is surrounded by a small number of angular starch grains which form an interrupted shell about it. Two contractile vacuoles, which contract alternately, are located in the anterior end of the cell. The contraction is rapid, but the interval between contractions is long as compared with that in ciliates. In a living cell the nucleus can be identified only as a small, spherical, nearly colorless region in the posterior part of the cell.

The thickness of the cell and the abundance of starch grains make it difficult to determine the shape of the chloroplast in living cells. In fixed and stained material it was not possible to distinguish between chloroplast and undifferentiated cytoplasm, and in the following discussion both will be included under the term "cytoplasm." The cytoplasm generally appears alveolar; in an occasional cell, however, it seems to be granular. In cross section a variable number of strands are visible extending from the peripheral cytoplasmic later to the pyrenoid, which is located centrally (fig. 4) or more or less laterally (fig. 5). In a cross section anterior to the pyrenoid, strands extend from the periphery and meet in the center forming a meshwork (fig. 6). It was not possible to determine whether the strands which extend from the peripheral portion of the cytoplasm to the pyrenoid belong to the chloroplast or to the undifferentiated cytoplasm. If to the latter, this would be one of the few species in which the pyrenoid is located outside the chloroplast, a condition reported by Kater (1929) for *Chlamydomonas*. It is probable, however, that *C. crucifera* possesses what is commonly described as an "H-shaped" chloroplast (really H-shaped in longitudinal section), the pyrenoid being imbedded in the strands running from the peripheral portion.

The longitudinal striations of the chloroplast are visible in whole mounts stained with Heidenhain's iron-alum haematoxylin or with Ehrlich's haematoxylin. When a living cell is seen from the anterior or posterior end there is some indication of ridges. In cross sections of fixed and stained material there is no such indication (figs. 4, 5, 6). Similar appearances in *Chlamydomonas* led Kater (1929) to suggest that the striated effect is produced as much by differences in opacity within the chloroplast as by the presence of actual ridges. It is possible that the difficulty in distinguishing between chloroplast and undifferentiated cytoplasm explains the apparent absence of ridges in cross sections of fixed material.

In a living cell the spherical pyrenoid is surrounded by a small number of concavo-convex bodies which give a starch reaction with iodine. After fixation with Schaudinn's fluid the pyrenoid shows a marked affinity for the Heidenhain stain, which colors it homogeneously black (figs. 8, 9). If preparations are stained with Bordeaux red before they are placed in haematoxylin, the pyrenoid becomes bright red. With Ehrlich's haematoxylin the pyrenoid is a light reddish purple. In either haematoxylin stain the pyrenoid is surrounded by a clear zone of varying thickness. This zone is probably occupied partially by the unstained shell of starch grains already mentioned. There is no indication of a reticulate structure of the pyrenoid or of radial strands traversing the hyaline zone about the pyrenoid, both of which were reported by Kater (1929) in *Chlamydomonas*. After Flemming's triple stain the bright red pyrenoid is surrounded by a layer of blue starch grains. The pyrenoid is stained light blue by crystal violet–iodine, while the surrounding starch grains are purple. Between the pyrenoid and the starch grains is a narrow hyaline zone (fig. 2). Several regions of the outer portion of the pyrenoid are usually stained dark blue (fig. 2). When these dark-staining

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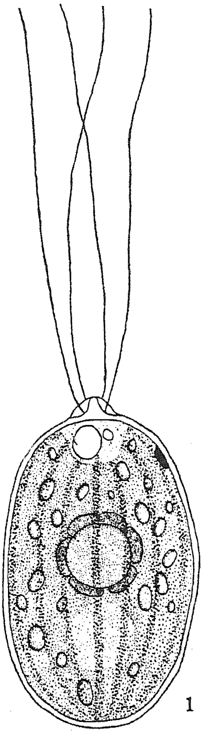
Explanation of figures 1–29

All drawings were made with a camera lucida; × 2550. Unless otherwise stated, all figures are from material fixed in Schaudinn's fluid.

FIG. 1. *Carteria crucifera* drawn from life. FIGS. 2, 3. Cells fixed in Randolph's modification of Navashin's fixative and stained with crystal violet-iodine, showing the pyrenoid with its outer transitional portion and the starch grains. FIGS. 4–10. Cells stained with Heidenhain's iron-alum haematoxylin. FIG. 4. Cross section showing centrally located pyrenoid. FIG. 5. Cross section with laterally located pyrenoid. FIG. 6. Cross section above level of pyrenoid. FIG. 7. Longitudinal section showing two blepharoplasts, contractile vacuoles and layer of cytoplasm between vacuoles. FIG. 8. Vegetative cell with two blepharoplasts, layer of cytoplasm between vacuoles, pyrenoid and nucleus. FIG. 9. Vegetative cell showing three blepharoplasts, layer of cytoplasm between contractile vacuoles, nucleus and pyrenoid. FIG. 10. Vegetative cell with two blepharoplasts, three pyrenoids and nucleus. FIGS. 11–14. Nuclei stained with Heidenhain's iron-alum haematoxylin. FIGS. 15–18. Nuclei stained with Ehrlich's haematoxylin showing number and arrangement of chromatic bodies. FIGS. 19–28. Nuclei stained with Feulgen's nucleal reaction. FIGS. 19–27. Nuclei showing number and arrangement of chromatic bodies. FIG. 28. Nucleus in position to divide between daughter pyrenoids. FIG. 29. Cell stained with Heidenhain's iron-alum haematoxylin. Stage in revolution of protoplast, pyrenoid constricting.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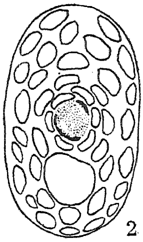
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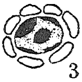
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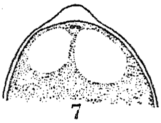
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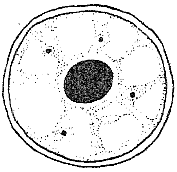
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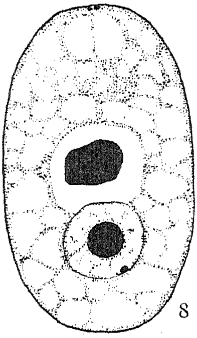
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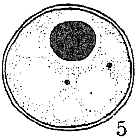
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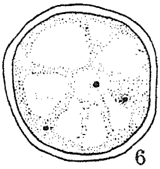
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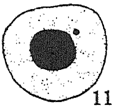
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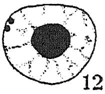
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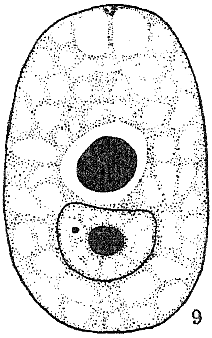
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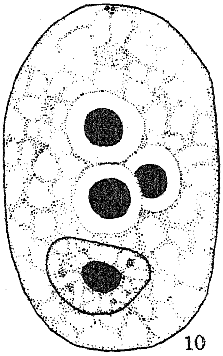
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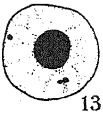
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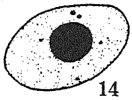
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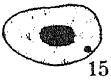
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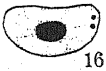
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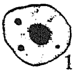
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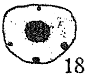
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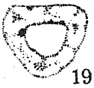
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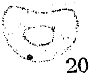
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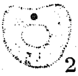
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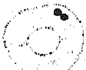
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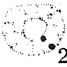
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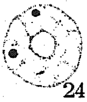
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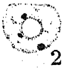
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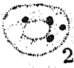
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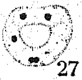
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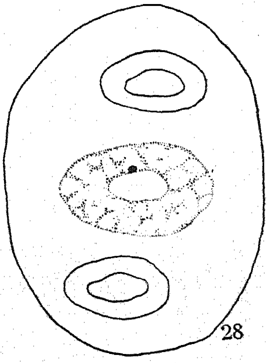
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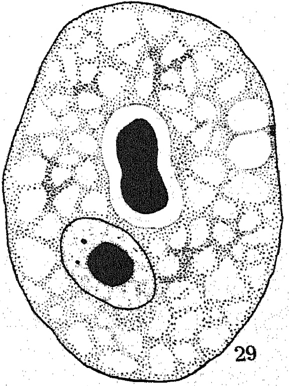
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regions are seen in surface view, the pyrenoid occasionally appears segmented or compound (fig. 3); however, the lighter blue central region is still visible. When a living cell is treated with iodine the outermost portion of the pyrenoid gives a starch-like reaction. Timberlake (1901) found that in *Hydrodictyon* tangential segments are cut off successively from the pyrenoid and that these segments are transformed into starch. G. M. Smith (1914) observed that one or more portions of the pyrenoid of *Scenedesmus* show a transitional staining reaction, which indicates that the pyrenoid may form several segments simultaneously and more than one starch grain at a time. It is possible that the dark-staining regions observed in the pyrenoids of *Carteria* stained with crystal violet–iodine or (in living cells) with iodine represent stages in the transformation of the pyrenoid substance into starch as reported by Timberlake for *Hydrodictyon,* Smith for *Scenedesmus,* and Bold (1931) for *Chlorococcum.*

Living cells which have undergone a period of growth since the last preceding division contain numerous shining oval bodies (fig. 1). Although these bodies resemble the starch grains about the pyrenoid in their refractive behavior, they do not give a starch reaction when living cells are treated with iodine. In preparations stained with crystal violet–iodine the cytoplasm contains many small, somewhat angular purple starch grains (fig. 2). These grains, the so-called "stroma starch," resemble the starch grains immediately about the pyrenoid in their reaction to crystal violet–iodine and in their angular shape. There seems to be little doubt that the oval bodies seen in the living cell, which, except for their failure to stain with iodine, resemble starch, are the bodies that are stained with crystal violet–iodine. It is possible that the "stroma starch" grains have changed chemically after their formation and hence do not give the typical starch reaction when living cells are treated with iodine. Frequently two layers of starch grains, instead of one, surround the pyrenoid (fig. 2), and the "stroma starch" tends to be concentrically arranged throughout the cell with respect to the pyrenoid. These facts may indicate that in *Carteria*, as in *Hydrodictyon*, all the starch grains within the cell have been formed from the pyrenoid, each layer in turn being forced away from the pyrenoid by the formation and separation of successive new layers.

Small rounded mitochondria appear in sections stained with Heidenhain's haematoxylin. They are imbedded in the cytoplasm, and often each appears to be surrounded by a very narrow clear region (figs. 4, 5, 6). Numerous cytoplasmic inclusions are visible in preparations of whole cells, but because of the thickness of the cell and the variety of intracellular bodies present identification of them has proved impossible.

The pigment spot is invisible in fixed material stained with either haematoxylin. When living cells are treated with iodine the pigment spot gives a starch-like reaction. It is possible that the pigment spot is stained with crystal violet–iodine, but if so it cannot be distinguished from the stroma starch grains. Franzé (1893) concluded that the pigment spot in the Chlorophyceae is composed of a number of highly refractive bodies of the nature of starch. Mast (1927) found that in unicellular members of the Volvocales the pigment spot consists of a spoon-shaped structure and a hyaline mass, the latter containing the photosensitive substance. Until the chemical nature of the substances composing the pigment spot is better known, no explanation can be offered for the starch-like reaction observed.

In fixed material stained with Heidenhain's or Ehrlich's haematoxylin, two blepharoplasts are visible, located just within the wall beneath the anterior papilla (figs. 8, 10). Occasionally a third one can be observed (fig. 9). Rarely, what appears to be a fourth blepharoplast is visible, but because of their arrangement in a single transverse plane, all four cannot often be seen at once. No cross sections were obtained which were certainly at the blepharoplast level.

When living cells are treated with iodine the contractile vacuoles increase in size, and the narrow layer of cytoplasm between them appears as a strand somewhat similar to the rhizoplast which has been figured for such forms as *Polytoma uvella* (Dangeard 1900, 1901; Entz 1913, 1918), *Chlamydomonas nasuta* (Kater 1929), *Haematococcus pluvialis* (Elliott 1934), and others. A similar layer of cytoplasm appears in cells fixed *in toto* and in longitudinal sections stained with either Heidenhain's or Ehrlich's haematoxylin (figs. 7, 8, 9, 10). In no case is it possible to trace this layer beyond the inner margins of the vacuoles. It seems clear that in *Carteria crucifera* a rhizoplast does not connect the nucleus with the blepharoplasts, and that the apparent strand in question is the layer of cytoplasm between the contractile vacuoles.

The nucleus is usually flattened and broader on its anterior side, which lies in contact with the pyrenoid. Posteriorly it is rounded and occasionally slightly elongate (figs. 9, 19, 21). In preparations subjected to Feulgen's nucleal reaction neither the nuclear membrane nor the nucleolus stains. The position of the nucleolus is indicated in such preparations by a colorless spherical or slightly elongated region in the center of the nucleus (figs. 19–28). The chromatin granules, stained purple or dark blue, form a sparse reticulum; occasionally the granules are concentrated or massed together and have the appearance of a large node (fig. 19). They are more numerous just within the nuclear membrane and about the nucleolus. The most conspicuous feature of the nucleus is the presence of one or more bodies, staining like chromatin, which are much larger than the granules obviously of chromatin. When a single body of this type is present, it may lie just within the nuclear membrane (fig. 20), beside the nucleolus (fig. 19), or at any point between nuclear membrane and nucleolus (fig. 21). If two bodies are present they may be so close together as to suggest a recent division of a single body (fig. 22); one may be just within the nuclear membrane and the other near the nucleolus (fig. 23); or they may be variously located (fig. 24). Frequently from one to three additional smaller bodies appear, likewise variously located (figs. 25, 26, 27). These smaller bodies stain in the same way as the chromatin granules and the two larger bodies described above, but they can be observed most readily in lightly stained preparations and in a cell which is not the product of a recent division.

In preparations stained with Heidenhain's or Ehrlich's haematoxylin the nucleolus and nuclear membrane are visible. The chromatin granules form a sparse network between the nucleolus and the nuclear membrane and are more numerous just within the membrane and immediately about the nucleolus. Here, also, from one to five bodies variously located can be observed (figs. 8–18). There seems little doubt that the bodies which stain darkly with the Feulgen technique and with either haematoxylin stain are the same, since they are identical in number, size, and position. In haematoxylin preparations the nucleolus obscures from view anything above or below it, and the numerous cytoplasmic inclusions often make it difficult to determine whether a particular body is in the nucleus or in the cytoplasm. Since neither the nucleolus nor any cytoplasmic structure is stained by the Feulgen method, it is not surprising that four or five bodies should be observed more frequently with this method than with the haematoxylin stains.

The cell undergoes a period of growth before dividing, sometimes becoming so large and thick that it is difficult to determine the position of the nucleus and the pyrenoid. The cell either withdraws or loses its flagella. The protoplast revolves through an angle of 90° so that the anterior clear zone comes to lie in contact with the former equatorial region of the cell wall. In living cells the occurrence of this revolution can occasionally be recognized from the changed position of the clear region and the contractile vacuoles. In fixed preparations, stages in the revolution of the protoplast can sometimes be identified by the position of the blepharoplasts, by the enlarged contractile vacuoles, and by the layer of cytoplasm between the vacuoles (fig. 29). The pyrenoid divides by constriction either before the revolution

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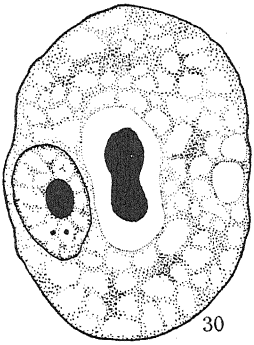
Explanation of figures 30–39

FIGS. 30–32. Cells stained with Heidenhain's iron-alum haematoxylin. FIG. 30. Nucleus in position to divide, pyrenoid constricting. FIG. 31. Nucleus in position to divide between daughter pyrenoids. FIG. 32. Lateral view of equatorial plate. FIGS. 33–38. Cells stained by Feulgen's nucleal reaction. FIG. 33. Lateral view of metaphase. FIGS. 34, 35. Polar views of equatorial plates. FIG. 36. Cell just after division, showing tightly appressed daughter protoplasts. FIG. 37. Two-celled colony. FIG. 38. Second division of colony just completed. FIG. 39. Palmella-like colony drawn from life.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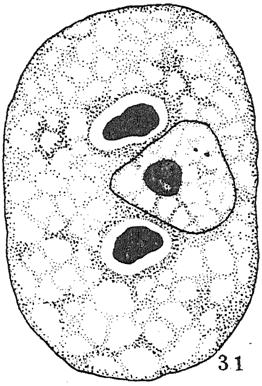
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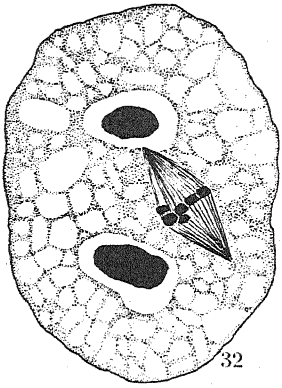
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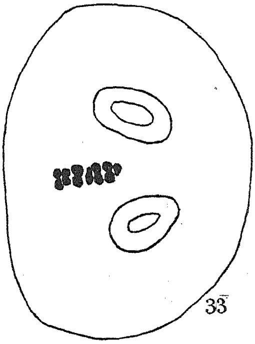
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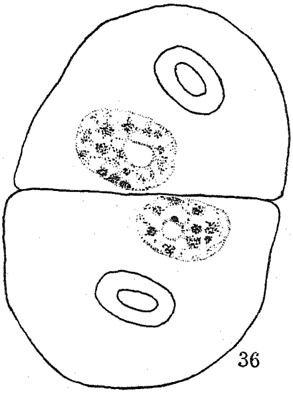
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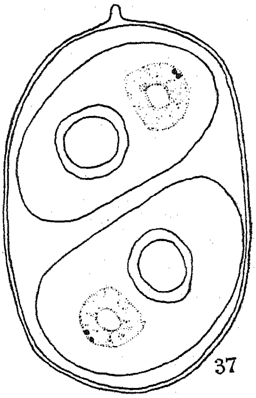
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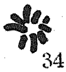
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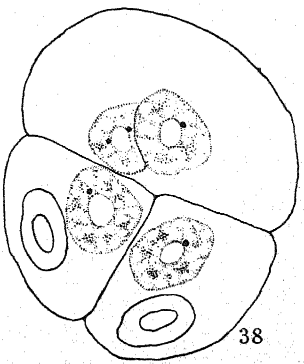
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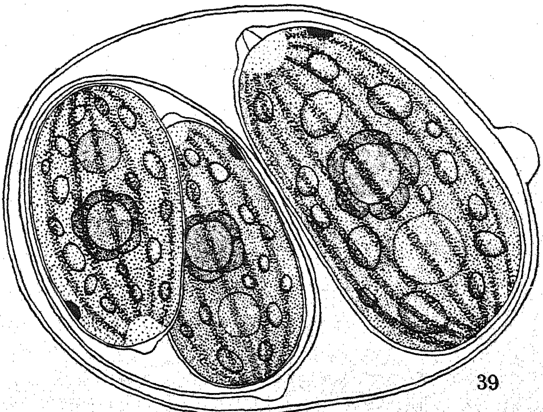
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of the protoplast or after the revolution is completed (figs. 29, 30). In consequence, a daughter pyrenoid is located toward each end of the cell and the nucleus lies between the daughter pyrenoids (figs. 28, 31). The increased size of the cell and the position of the nucleus between the daughter pyrenoids are the most satisfactory criteria for recognizing a cell which is about to divide.

A few cells were observed which contained two or even three pyrenoids (fig. 10) but which had not become enlarged and showed no indication of a revolution of the protoplast. One cell contained one pyrenoid and two nuclei, both located in the posterior part of the cell. Another cell possessed three pyrenoids in its central region and two nuclei in the posterior part. Neither cell had enlarged nor had its protoplast revolved. Although two pyrenoids are typically found only in cells which are about to divide, it appears that the pyrenoid can divide at any time to form two or three bodies. Also the nucleus may divide without a preceding revolution of the protoplast or division of the pyrenoid, and nuclear division is not always followed by cell division.

A nucleus which is preparing to divide is enlarged and usually elongate (figs. 28, 30). Such a nucleus resembles in structure a resting nucleus, and the darkly staining bodies previously described are still visible (figs. 28, 29). As the nucleus enters the prophases the chromatin granules appear more numerous and massed together, and it soon becomes impossible to distinguish the larger bodies observed in the resting nucleus. The nucleolus disappears and definitely organized chromosomes gradually appear.

Nine chromosomes are visible in a late prophase or in polar views of the equatorial plate. Three of these are about three times as long as wide and often curved, three about twice as long as wide, and three only slightly longer than wide (figs. 34, 35). In a lateral view of an equatorial plate the chromosomes appear short and somewhat bean-shaped (fig. 32).

The sharply pointed spindle lies either longitudinally or obliquely oriented between the daughter pyrenoids in the middle of the cell (fig. 32). The smallness of the division figures prevents the determination in lateral view of whether there are fibers extending from pole to pole in addition to those running from poles to chromosomes. There is no indication of a body of any nature at either pole of the spindle in Feulgen preparations (fig. 33) or with either of the haematoxylin combinations used (fig. 32).

The daughter chromosomes separate and move toward the respective spindle poles. After they reach the poles they become less distinct and appear massed or clumped. In connection with each daughter group the nuclear membrane and nucleolus appear. In Feulgen preparations the chromatin granules appear large and closely packed; there is little indication of a reticulum (fig. 36). This condition persists for some time.

The protoplast divides by constricting between the newly formed daughter nuclei. Although this appears to be a transverse division, it divides the protoplast longitudinally because of the previous revolution.

The cell may quickly divide a second time, or the two daughter protoplasts may develop walls while still within the mother-cell wall. The daughter cells shift positions within the mother-cell wall and usually come to lie with their anterior ends oppositely placed (fig. 37). They develop flagella which can be seen to be curled around each daughter cell and beating slightly. The daughter cells are freed by a local disintegration of the mother-cell wall.

If a second division follows, the daughter nuclei formed by the first division do not assume a typical resting condition, and the daughter cells do not form visible walls but remain tightly appressed. The second division is similar to the first, but it is more difficult to follow because of the crowding of the nuclear contents within a smaller space. It is uncertain whether a revolution of the daughter protoplasts occurs. The two nuclei do not always divide simultaneously; one may be at the equatorial-plate stage while the other is in an early prophase. The two daughter cells divide in planes at right angles to each other and to the plane of the first division.

A third division also may follow, or the four daughter protoplasts formed by the second division may develop walls. In the latter case the cells shift within the mother-cell wall and become variously arranged. The mother wall breaks down and the cells are liberated. If a third division follows the second, it is very similar to the first and second divisions, but the nuclei and pyrenoids are usually so close together that the story cannot be followed in detail. Eight small daughter protoplasts are finally formed, which develop walls and flagella. The mother wall breaks down and liberates the cells of the colony.

It was impossible to follow the blepharoplasts after the revolution of the protoplast was complete or to observe their formation and the growth of the flagella. Few colonies of sixteen cells were observed. Gametes were obtained only once during the course of this study. All later attempts by varying the nutrient concentration, illumination, and temperature failed to induce their formation. Either environmental conditions have not been suitable or else the strain is heterothallic. When gametes were formed the cultures were being watered with lake water, and it is possible that the second strain may have been introduced with the water.

Palmella-like colonies, consisting of several colonies within a mother wall, are occasionally formed in cultures growing on agar. These colonies are never very large, and the walls do not become noticeably gelatinous (fig. 39). When such colonies are placed on sand, the colonial walls break down and the enclosed daughter cells develop flagella and become free-swimming.

DISCUSSION

The neuromotor apparatus. Most investigators who have described blepharoplasts in the Volvocales report the presence of either one or two. Even quadriflagellate species seem generally to possess but two. In *Carteria crucifera*, however, certainly three and in all probability four blepharoplasts are present.

A cytoplasmic strand extending from the bases of the flagella toward the nucleus was described by Dangeard (1898) in *Phacotus angulosus*, *Chlorogonium euchlorum*, *Cercidium elongatum*, and *Chlamydomonas variabilis*. Later (1900, 1901) he referred to a similar structure in *Polytoma uvella* as a "rhizoplast." Rhizoplasts, connecting the blepharoplasts with the nucleus, have been described by Prowazek (1901) and Entz (1913, 1918) in *Polytoma uvella*, by Kater (1929) in *Chlamydomonas nasuta*, by Elliott (1934) in *Haematococcus pluvialis*, by Hovasse (1937) in *Eudorina* (*Pleodorina*) *illinoisensis*, and (somewhat doubtfully) by Hartmann (1919) in *Chlorogonium elongatum* and by Kater (1925) in *Polytomella citri*. Two rhizoplasts, one extending from each blepharoplast toward the nucleus, were reported by Mast (1916) for *Eudorina* sp. and by Hartmann (1921) for *E. elegans*.

In *Carteria crucifera* a strand which might be taken for a portion of a rhizoplast is visible between the contractile vacuoles. This strand, however, cannot be traced beyond the inner margins of the vacuoles. It seems clear that what is seen here is the layer of cytoplasm between the contractile vacuoles. This is the only species thus far investigated in which the nucleus is posterior to the pyrenoid. It is possible that in forms in which the nucleus is anterior, the narrow layer of cytoplasm between the vacuoles, erroneously interpreted as a rhizoplast, has been thought to extend to the nucleus.

An intranuclear centrosome whose division products appear at the poles of the spindle has been reported by Prowazek (1901) and Entz (1913, 1918) in *Polytoma uvella*, by Hartmann (1904) in *Volvox globator*, by Zimmermann (1921) in *V. aureus*, and by Kater (1929) in *Chlamydomonas nasuta*. Chatton (1910) described a centrosome within the nucleolus (karyosome) in *Pleodorina californica*. Elliott (1934) found an extranuclear centrosome which functions as a division center in *Haematococcus pluvialis*. Centrosomes were observed at the poles of the spindle by Aragão (1910) in *Polytomella agilis* and by Hartmann (1919) in *Chlorogonium elongatum*. Kater (1925) found no centrosomes in the resting nuclei of vegetative cells of *Polytomella citri*, although centrosomes appeared at the poles of the spindle. In encysted cells, however, extranuclear centrosomes were visible. In all these species the centrosomes and blepharoplasts, commonly connected by a rhizoplast, are reported to function in their distinctive capacities. In *Eudorina* (*Pleodorina*) *illinoisensis* according to Hovasse (1937), the two blepharoplasts migrate from the bases of the flagella to the nucleus, move along the nuclear membrane to opposite sides of the nucleus and determine the respective poles of the spindle. After division each body moves to the anterior end of its daughter cell and divides to form two blepharoplasts. This is the only example among the Volvocales of a body reported to function as both centrosome and blepharoplast. Hovasse saw in the nucleus of this species from one to three bodies which are connected with the nucleolus by strands. He suggested that they be called "satellites of the nucleolus."

No bodies were observed at the poles of the spindle by Dangeard (1898, 1900, 1901) in several species of *Chlorogonium, Cercidium, Lobomonas, Phacotus, Chlamydomonas,* and *Carteria,* and in *Polytoma uvella,* by Merton (1908) in *Pleodorina illinoisensis,* by Reichenow (1910) in *Haematococcus pluvialis,* by Jameson (1914) in *Parapolytoma satura,* by Doflein (1916, 1918) in *Polytomella agilis,* or by Bělař (1921) in an unidentified species of *Chlamydomonas.*

In *Carteria crucifera* from one to five rather conspicuous bodies are variously located within the nucleus. There is no evidence that they are connected with the nucleolus. The bodies are most consistently and easily observed in Feulgen preparations. Although they are stained by haematoxylin, the darkly stained nucleolus and the cytoplasmic inclusions sometimes make their recognition difficult. There is no indication of a body at either pole of the sharply pointed spindle. It is possible that in previous studies one of these intranuclear bodies has been identified as a centrosome and that two of them have been interpreted as the product of a recent division of a centrosome. The Feulgen technique has not previously been employed extensively in investigating members of the Volvocales. In view of their reaction to this technique, it is suggested that the structures in question are chromocenters and that they are similar to the bodies observed by Hovasse in *Eudorina (Pleodorina) illinoisensis.* The term "chromocenter" seems suitable, for these bodies appear to be definite chromatic regions which remain condensed and highly chromatic during the resting stage.

The nucleolus. A chromatin-containing nucleolus which fragments to form the chromosomes was described by Jameson (1914) in *Parapolytoma satura* and by Kater (1925) in *Polytomella citri.* Kater (1929) held that the cortical portion of the nucleolus of *Chlamydomonas nasuta* contains chromatin. The nucleolus of *Carteria crucifera* contains no chromatin. Feulgen preparations show the nucleolus as a non-chromatic spherical body surrounded by an accumulation of chromatin granules. It is possible that it was the aggregation of granules about the nucleolus which led Kater to his conclusion.

Mitotic phenomena. Hartmann (1919) described in *Chlorogonium elon-*

gatum the formation of a half-spindle, which is followed by the division of both centrosome and half-spindle. One half-spindle and its centrosome migrate along the nuclear membrane to the opposite side of the nucleus from the position of the sister centrosome and half-spindle. The same author (1921) found that in the first division of *Eudorina elegans* the spindle is formed in the typical fashion, but that in the second division of some cells a half-spindle appears whose behavior is similar to that seen in *Chlorogonium*. In *Carteria crucifera* spindle-formation is of the typical sort.

In *Polytoma uvella*, according to Entz (1913, 1918) the flagella and blepharoplasts persist during the early stages of division but eventually disappear. After mitosis a body buds off from the nucleolus, divides, and one division product remains in the nucleus as the centrosome, while the other migrates to the anterior end of the cell, the rhizoplast appearing behind it. At the anterior end it divides to form two blepharoplasts. Kater (1929) and Elliott (1934) found that in *Chlamydomonas nasuta* and *Haematococcus pluvialis* the flagella and blepharoplasts disappear during division. After the division is completed a body buds off from the centrosome and migrates to the anterior end of the cell, remaining connected with the centrosome by a rhizoplast. This body divides to form the two blepharoplasts. Aragão (1910) and Doflein (1916, 1918) report that in *Polytomella agilis* one blepharoplast and two flagella pass to each daughter cell during division. Each blepharoplast then divides and two additional flagella are formed in each daughter cell. According to Jameson (1914), in *Parapolytoma satura* the blepharoplasts and flagella pass during cell division to a single daughter cell. In the daughter cell which does not receive these structures, a body buds off from the nucleolus, divides, and the daughter halves migrate to the anterior end where they become blepharoplasts. Kater (1925) reported that in *Polytomella citri* the blepharoplasts persist and divide during the division of a vegetative cell. In an encysted cell a new centrosome and blepharoplasts are formed by a bud from the nucleolus which divides. One division product remains outside the nucleus, supposedly as the centrosome, while the other migrates to the anterior end of the cell and divides to form the blepharoplasts. Hovasse (1937) found that in *Eudorina* (*Pleodorina*) *illinoisensis* the two blepharoplasts, after cell division, migrate from the poles of the spindle to the anterior ends of the respective daughter cells and divide.

In *Carteria crucifera* it was not possible to follow the blepharoplasts after the revolution of the protoplast was completed. No stages were observed which indicated the budding off of a body from the nucleolus. The blepharoplasts do not stain with Feulgen's nucleal reaction; they seem to have no relation to the bodies present in the nucleus.

Kater (1929) observed a revolution of the protoplast before mitosis through an angle of 90° in *Chlamydomonas nasuta*. A similar revolution occurs in *Carteria crucifera*.

Dangeard (1898) reported the following chromosome numbers: *Chlamydomonas Dilli* 10, *C. variabilis* 10, *C. monadina* 30, *Carteria cordiformis* 12. Pascher (1916) found 10 chromosomes in an unidentified species of *Chlamydomonas.* Eight chromosomes are figured by Bělař (1926) in an unnamed *Chlamydomonas.* Moewus (Hartmann 1934) observed 10 in *Chlamydomonas eugametos,* in *C. paupera,* and in a hybrid between *C. eugametos* and *C. paupera. Carteria crucifera* has nine. There is apparently no relation between the number of chromosomes and the number of flagella in *Chlamydomonas* and *Carteria.* Species of the biflagellate *Chlamydomonas* thus far investigated have chromosome counts ranging from eight to thirty. The two species of the quadriflagellate *Carteria* which have been studied have counts of nine and twelve chromosomes.

SUMMARY

The chloroplast of *Carteria crucifera* is H-shaped in longitudinal section; strands extend from the periphery to the central region where the pyrenoid is located.

The outermost portion of the pyrenoid at times stains differently from the remainder; this differentiated portion may represent a transition stage in the transformation of the pyrenoid substance into starch. The occurrence of two layers of starch grains close about the pyrenoid and the variation in staining reaction of the pyrenoid indicate that from it are formed all the starch grains within the cell.

Three, occasionally four, blepharoplasts are visible at the bases of the flagella. In fixed material the contractile vacuoles are enlarged and the layer of cytoplasm between them resembles a rhizoplast. In no case is it possible to trace this layer or strand beyond the inner margins of the contractile vacuoles.

The nucleus has a distinct membrane, a large nucleolus, and chromatic material in the form of strands and knots or granules. The nucleolus contains no chromatin. Within the nucleus are from one to five variously located bodies which are larger than the granules obviously of chromatin, yet which stain like chromatin with Feulgen's nucleal reaction and with haematoxylin. It is suggested that these bodies are chromocenters.

Nuclear division is preceded by a revolution of the protoplast through an angle of 90° and by the division of the pyrenoid by constriction. There is no indication of a centrosome at either pole of the spindle, which lies longitudinally or obliquely between the daughter pyrenoids. The protoplasm divides by constriction.

There is apparently no relation between the number of chromosomes and the number of flagella. *Carteria crucifera* has nine chromosomes.

WARREN, ILLINOIS

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BIOTIN AND THE GROWTH OF FUSARIUM AVENACEUM[1]

William J. Robbins and Roberta Ma

(WITH SIX FIGURES)

Vitoria (21) reported in 1939 that *Fusarium avenaceum* did not grow in a liquid medium containing per liter 7.2 g. cane sugar, 3.6 g. dextrose, 1.23 g. $MgSO_4 \cdot 7\ H_2O$, 2.72 g. KH_2PO_4, and 2.02 g. KNO_3, but grew on the same medium solidified with agar. Other species of *Fusarium* grew well in the liquid medium. Vitoria found further that the addition to his medium of the filtrate from a six-day-old culture of *Penicillum sp.* permitted the development of *F. avenaceum*. As little as 0.25 ml. of the *Penicillum* filtrate was effective though the benefit increased with additions up to 50 ml. of filtrate.

The nitrogen in the basic medium used by Vitoria was in the form of nitrate, which is a poor source for some fungi (14). It might be suggested that the benefit observed from the filtrate of the *Penicillum* culture was due to organic nitrogen derived from that fungus. However, 0.25 ml. of the filtrate must have contained very little organic nitrogen. This consideration suggested that the failure of *F. avenaceum* to grow in the liquid medium might have been the result of growth substance deficiencies which were supplied by the agar or by the *Penicillum* filtrate. One of the authors has been interested in the growth substances in agar (13, 16) and the effect of agar on *F. avenaceum* seemed worthy of further investigation.

MATERIALS AND METHODS

Three strains of *F. avenaceum* were obtained. One was kindly supplied by Dr. E. C. Stakman; it will be referred to as strain (M). The second was secured through the courtesy of Dr. R. W. Goss and will be called strain (N). The third was obtained through the kindness of Dr. Vitoria and will be called strain (V). The three strains differed in appearance of colony, pigment production, and size and shape of conidia. The (M) and (N) strains were much alike and both produced conidia which were from 1 to 3 celled and inclined to be straight with blunt ends. The (V) strain formed reddish pigment freely and the conidia were from 5 to 7 celled, curved, and with pointed ends.

Three basic media were used as follows:

Solution 1 contained per liter of distilled water 50 g. dextrose, 1.5 g. KH_2PO_4, 0.5 g. $MgSO_4 \cdot 7\ H_2O$, and 2.0 g. asparagine; solution 2 was Vi-

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[1] Supported in part by a grant from the Josiah Macy Jr. Foundation.

toria's liquid medium; solution 3 was solution 1 with 1.76 g. of $(NH_4)_2SO_4$ instead of asparagine. This quantity of $(NH_4)_2SO_4$ contained the same amount of nitrogen as the 2 g. of asparagine.

The dextrose was Corn Products C.P.; the asparagine was purified by treatment with Norit A and recrystallization from alcohol; the other chemicals were of C.P. grade unless specifically noted. All glassware was pyrex, cleaned with chromic acid cleaning mixture and thoroughly rinsed with tap

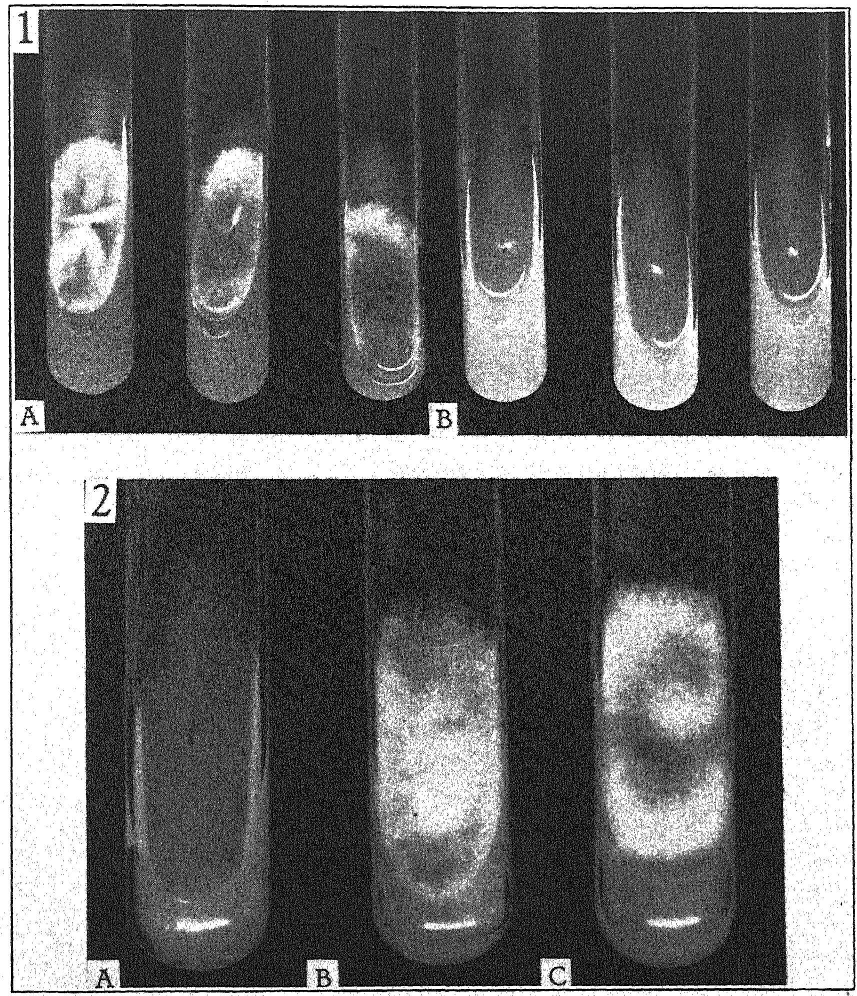

FIG. 1. *F. avenaceum*, strain (V), on solution 2 plus (A) 1.5% Difco agar (B) 1.5% purified Difco agar. Age of cultures 3 days. FIG. 2. Three strains of *F. avenaceum* on solution 2 plus 1.5% purified Difco agar: A, strain (V); B, strain (N); C, strain (M). Age of cultures 4 days.

and distilled water. Media were sterilized at 12 pounds pressure for 20 minutes. For inoculation a bit of mycelium approximately a square mm. in area was removed from a culture on agar; care was taken to transfer none of the agar. In some instances conidia instead of mycelium were used for inoculation. Cultures were incubated at 25° C. in the dark.

EXPERIMENTS

Growth in liquid cultures. Vitoria's report that his strain of *F. avenaceum* does not grow in his liquid medium was confirmed. Triplicate cultures containing 25 ml. of solution 2 in 125 ml. Erlenmeyer flasks were inoculated with bits of mycelium from a culture of strain (V) on a thiamin-peptone agar (18). Growth in a period of 7 days was slight and subcultures into solution 2 failed completely. The same results were secured with solution 1 in which the nitrogen was supplied as asparagine.

Strain (M) grew well in solution 1, in which it produced a greenish yellow pigment. It was carried for four successive passages in this solution and showed no evidence of reduced growth in the fourth passage. Similar results were secured with solution 2, though the growth was not so vigorous as in solution 1 and no pigment was produced.

Strain (N) grew well in solution 1 through four successive passages but produced less pigment in the solution than strain (M). Its growth was as vigorous as that of strain (M). Strain (N) grew in solution 2 also but less well than in solution 1.

From this experiment it appeared that the three strains differed in their growth responses and that a solution in which strain (M) and (N) grew quite well was unsatisfactory for strain (V).

Effect of agar. Solution 2 was solidified with 1.5 per cent agar and approximately 8 ml. placed in test tubes, sterilized, and sloped. Triplicate tubes of four types of agar were used as follows:

1. A sample of Difco standardized granulated agar.
2. The same agar purified by extraction with 5 per cent aqueous pyridine and alcohol.[2]
3. A sample of Eimer and Amend flake agar.
4. The same agar purified by extraction with pyridine and alcohol.

Strain (V) grew well on solution 2 plus 1.5 per cent Difco agar; the mycelium nearly covered the surface of the slope in three days. It grew little or not at all when the purified agar was substituted for the unpurified agar (fig. 1). Similar results were obtained with the purified and unpurified Eimer and Amend flake agar, though the organism grew less rapidly on the medium solidified with the unpurified flake agar than on that in which unpurified Difco agar was used.

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[2] The agar was purified as follows: 1 pound of agar was treated in a percolator with 12 liters of 5 per cent aqueous distilled pyridine; the final percolate was colorless. The agar was then washed with 2 liters of ethyl alcohol and boiled with 12 liters of ethyl alcohol. It was filtered through a Buchner funnel and dried at 50–60° C. The percolate and washings were combined, evaporated to remove the pyridine and alcohol, and made up to volume with distilled water so that 1 ml. of the extract was equivalent to 1 gram of the extracted agar.

Strains (M) and (N) grew on the media solidified with all four types of agar (fig. 2), but the growth on media made with the purified agars was less rapid than on that made with either of the unpurified agars.

Subcultures of each strain on each type of agar were carried for three successive passages[3] with no significant differences between the growth on a particular medium in successive passages. The development of strain (M) was much like that of strain (N); white cottony aerial mycelium formed on the agar slopes and little pigmentation was observed. The aerial mycelium of strain (V) grown on the unpurified agars was less luxuriant than that of strain (M) and (N) and considerable pink color was formed.

Effect of agar extract on growth of strain (*V*). The failure of strain (V) to grow satisfactorily on media made with the purified agars was because of the removal of some beneficial principle from the agar in the purification. This was demonstrated by observing the effect on its growth of additions of the agar extract to the purified agar. Solution 2 with 1.5 per cent purified Difco agar was prepared. To some tubes extract[4] was added equivalent to 1 per cent, 5 per cent, or 15 per cent agar. The organism made little or no

TABLE 1

Growth of strain (V) of F. avenaceum on agar slopes of solution 2 plus 1.5% purified Difco agar to which various supplements were added. For details see text.

Additions to solution 2 plus 1.5% purified agar	Diameter of colonies in cm.	
	2 days	3 days
None	No growth	No growth
5 supplements	1.3	2.5
7 supplements	No growth	No growth
12 supplements	1.0	2.0
Extract equivalent to 1% agar	1.95	3.8
Extract equivalent to 5% agar	2.4	3.8
Extract equivalent to 15% agar	2.2	3.5
Biotin	1.3	2.5
Ca fraction	1.7	3.0
Dr fraction	No growth	No growth
Ca & Dr fraction	2.4	4.0

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[3] The growth of strain (V) on the media made with purified agars was so poor in the first passage that no attempt was made to carry it beyond the second passage on the purified agar.

[4] The extract contained 10 per cent dry matter of which about 15 per cent was ash.

growth on the purified agar but grew well on the purified agar to which the agar extract was added (table 1). Rapid growth occurred in all tubes containing agar extract and in less than a week the slope was covered with mycelium and an orange-colored mass of spores occupied an area 1 cm. or more in diameter on those cultures with extract equivalent to 15 per cent agar (fig. 3). A similar but somewhat smaller area of spores was formed on the cultures with extract equivalent to 5 per cent agar. None was observed in the tubes with 1.5 per cent unpurified agar or on those containing purified agar and extract equivalent to 1 per cent agar.

Effect of various growth substances on strain (*V*). There appeared to be something extracted from the agar which induced growth of strain (V). This material or materials was not effective through modifying the pH since the hydrion concentration of media made with the purified and unpurified agar was found to be the same. It was thought not to be a mineral nutrient or to serve as a source of nitrogen because mineral salts and a nitrogen source were added to both the purified and unpurified agars and, further, the nitrogen compounds in agar are relatively unavailable. The effect of various growth substances was, therefore, determined.

The following media were prepared in tubes; six replications of each medium were used. The source of each growth substance and the quantity used per tube are given below:

1. Solution 2 with 1.5 per cent purified Difco agar.
2. Solution 2 with 1.5 per cent purified Difco agar plus thiamin, Merck's synthetic, 10 millimicromoles; pyridoxine, Merck's synthetic, 20 millimicromoles; calcium pantothenate, Merck's synthetic, 5 micrograms; biotin,[5] du Vigneaud, 0.004 microgram; nicotinamide, S.M.A., 10 micrograms.
3. Solution 2 with 1.5 per cent purified Difco agar plus para-aminobenzoic acid, Eastman, 5 micrograms; pimelic acid, Eastman, 5 micrograms; i-inositol, Pfanstiehl, 10 mgm.; riboflavine, Labco natural, 10 millimicromoles; glutamine, György, 10 micrograms; 2-methyl-l, 4-naphthoquinone (S.M.A.) 5 micrograms; ascorbic acid, Merck's natural, 5 micrograms.
4. Solution 2 with 1.5 per cent purified Difco agar plus the 12 growth substances.

Two days after inoculation there was no growth on medium 1, the colonies on medium 2 averaged 1.3 cm. in diameter, no growth appeared on medium 3 and on medium 4 the colonies averaged 1.0 cm. in diameter (table 1). At the end of a week very little growth had occurred on media 1 and 3; the surface of the agar slopes of media 2 and 4 was covered with mycelium though the growth was somewhat less vigorous on medium 4 than on medium 2.

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[5] The biotin was a pure preparation of the methyl-ester supplied through the courtesy of Dr. Vincent du Vigneaud and described in a recent publication (5).

These results indicated that one or more of the five growth substances in the mixture used in medium 2 induced growth of strain (V) on solution 2 prepared with 1.5 per cent purified agar. Biotin methyl-ester was found to be the effective substance.

Effect of biotin on growth of strain (V). The growth of strain (V) on solution 2 solidified with 1.5 per cent purified agar plus 0.004 microgram of biotin per tube containing 8 ml. of medium was found to be about equal to that on the same medium plus pyridoxine, thiamin, calcium pantothenate, and nicotinamide in addition to the biotin. Growth in the tubes containing biotin was, however, less rapid than on media containing agar extract equivalent to 1 per cent agar (table 1).

These observations demonstrated that the growth of strain (V) on media prepared with the purified agar was poor because the organism suffered from a biotin deficiency. It appeared that sufficient biotin was present in the unpurified agar to satisfy the deficiency and that the biotin was removed from the agar by the method of purification used.

However, the addition of agar extract to the purified agar seemed to be more effective than the addition of the 0.004 microgram of pure biotin. Why should this be? Several possibilities must be considered. Perhaps the amount of biotin added in the extract equivalent to 1 per cent agar was greater than the 0.004 microgram of pure biotin used per tube in the experiment described above. *F. avenaceum* may exhibit partial deficiencies for growth substances other than biotin which are supplied by the agar extract. If so, the substances involved are not pyridoxine, pantothenic acid, thiamin, or nicotinamide, since growth with these four supplements in addition to biotin was about the same as with biotin alone. It is probable also that they are not included in the second group of seven since the growth when all twelve growth substances were used was not better than when the biotin alone was present (table 1). The minerals in the agar extract may have been important or some other factor may have played a role. Some of these possibilities were investigated.

Effect of quantity of biotin. Tubes of solution 2 with 1.5 per cent purified agar were prepared. To some tubes extract equivalent to 0.5 per cent, 1.0 per cent, 5 per cent, or 15 per cent agar was added; to others biotin was added in the following amounts per tube: 0.001, 0.005, 0.01, 0.05, or 0.1 microgram. Eight mgs. of asparagine were added to some tubes containing 0.05 microgram or 0.1 microgram of biotin. The experiment was performed in triplicate and carried for two successive passages. The second passage was started when the cultures in the first passage were three days old. Tubes of each kind of medium in the second passage were inoculated from the growth in tubes of the same kind of medium in the first passage.

TABLE 2

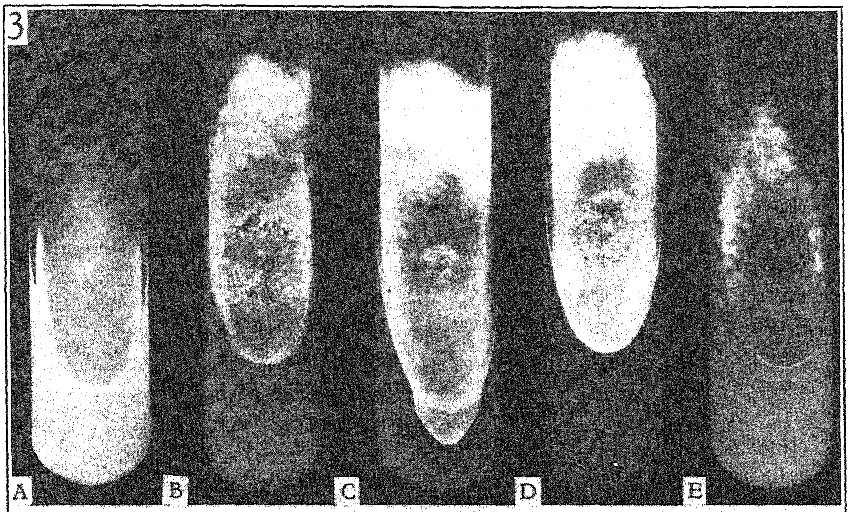
Growth of strain (V) of F. avenaceum on agar slopes of solution 2 plus 1.5% purified Difco agar to which various supplements were added.

Additions to 8 ml. of solution 2 plus 1.5% purified agar	Diameter of colonies cm.			
	1st passage		2nd passage	
	2 days	3 days	2 days	3 days
None	0.6	0.6	No growth	No growth
Extract equivalent to 0.5% agar	2.0	3.5	1.6	2.9
Extract equivalent to 1.0% agar	......	......	1.9	3.1
Extract equivalent to 5.0% agar	2.3	3.7	2.0	3.4
Extract equivalent to 15.0% agar	2.3	4.0	......	......
0.001 microgram biotin	0.6	1.1	No growth	0.4
0.005 microgram biotin	2.0	3.3	1.5	2.7
0.01 microgram biotin	2.0	3.1	1.4	2.5
0.05 microgram biotin	1.9	3.5	1.4	2.3
0.1 microgram biotin	1.9	3.3	1.5	2.5
0.05 microgram biotin and 8 mgm. asparagine	1.6	2.9	1.2	2.1
0.1 microgram biotin and 8 mgm. asparagine	1.5	2.7	1.3	2.3

In the first passage there was some growth at the expense of the original inoculum on the purified agar, but little or no growth occurred in the second passage (table 2). The effect of 0.001 microgram of biotin per tube was slight; 0.005 microgram produced considerable growth and as far as colony diameter was concerned there was little difference between the effects of 0.005 microgram and 0.1 microgram of biotin. The heaviness of growth, however, increased as the amount of biotin increased (fig. 4). The addition of asparagine reduced the rapidity of growth. Even with 0.1 microgram of biotin per tube the diameter of the colonies was less than with extract equivalent to 1 per cent agar. This suggested that although biotin is the material primarily responsible for the effectiveness of agar in causing growth of strain (V) there are other soluble substances in the agar which favorably affect growth of the organism in the presence of biotin. This assumption is supported by comparing the growth *F. avenaceum* in liquid cultures containing pure biotin with that in cultures containing agar extract with known biotin content.

Quantity of biotin in Difco agar. The quantity of biotin in the extract of Difco agar was estimated by the growth of *Ashbya gossypii* as described by Robbins and Schmidt (15). Various quantities of the agar extract or of biotin (table 3) were added to 25 ml. quantities of the solution used by Robbins and Schmidt and the hydrion concentration was adjusted with

Na_2HPO_4 so that it was pH 5.6 after sterilization. The cultures were inoculated with a suspension of *Ashbya* and incubated at 25° C. for 15 days. Dry weights were determined by filtering into Gooch crucibles and drying at 100° C. The biotin was estimated by the curve given by Robbins and Schmidt. The experiment was performed in triplicate.



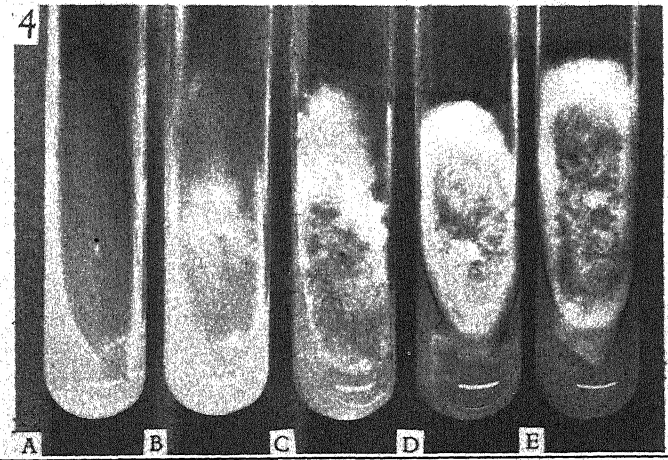


FIG. 3. *F. avenaceum,* strain (V), on solution 2 with 1.5% purified Difco agar plus (A) nothing, (B) extract equivalent to 1% agar, (C) extract equivalent to 5% agar, (D) extract equivalent to 15% agar, (E) 0.004 microgram biotin per tube. Age of cultures 6 days. FIG. 4. *F. avenaceum,* strain (V), on solution 2 with 1.5% purified Difco agar plus (A) nothing, (B) 0.001 microgram biotin, (C) 0.005 microgram, (D) 0.01 microgram, (E) 0.1 microgram per tube. Age of cultures 6 days.

Some growth occurred in the check solution probably at the expense of biotin carried over with the inoculum which came from an agar containing thiamin and peptone. However, 0.005 microgram of biotin increased growth and 0.01 microgram gave a further increase. A favorable effect of 0.025 ml. of agar extract containing 2.5 mg. dry matter was observed and further benefits were obtained up to 0.625 ml. of agar extract per flask. Growth was less with 1.25 ml. of agar extract per flask than with 0.625 ml., evidently because of some inhibitory action of this quantity of material.

In the fourth and fifth columns of table 3 the quantity of biotin in the agar extract added per culture and the quantity of biotin per ml. of agar extract as calculated from the growth of *A. gossypii* are given.

TABLE 3

Growth of Ashbya gossypii in solutions supplemented with agar extract or pure biotin and the quantity of biotin in the agar extract as estimated from the growth of Ashbya.

Additions to 25 ml. of Robbins and Schmidt solution	Av. dry wt. Ashbya per culture mg.	Net dry wt. Ashbya per culture mg.	Biotin per culture milli-micrograms	Biotin per ml. agar extract milli-micrograms
1.25 ml. agar extract	20.3	15.5	......	....
0.625 ml. agar extract	41.0	36.2	58	92.8
0.25 ml. agar extract	24.5	19.7	24	96.0
0.125 ml. agar extract	16.9	12.1	9.9	79.9
0.025 ml. agar extract	10.3	5.5	2.8	112.0
None	4.8	....	......	....
0.005 microgram biotin	12.8	8.0	......	....
0.01 microgram biotin	15.2	10.4	......	....

The average amount of biotin per ml. of agar extract as estimated by this means was 0.095 microgram. Since 1 ml. of the extract was equivalent to 1 g. of original agar the biotin content of the original agar also was 0.095 microgram or 1 g. of biotin in about 10,526 kg. of agar.[6]

Kögl and Tonnis (8a) estimated 1 g. of biotin in 3,125 kg. of dried egg yolk. On the basis of these figures the Difco agar we used contained about one-third as much biotin as dried egg yolk, the source from which Kögl and Tonnis originally isolated it.

In the experiments described above in which agar extract or biotin was added to pure agar it was observed that the growth in 8 ml. of medium containing 1 per cent agar extract was somewhat better than in the same quantity of medium plus 0.004 microgram of biotin. Eight ml. of 1 per cent agar extract contained 0.08 ml. of agar extract, or 0.0076 microgram of biotin, a quantity sufficient to give the results observed.

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[6] Du Vingneaud, using growth of yeast for bio-assay, found the biotin content of this agar extract to be 0.041 microgram per ml., about one-half the value we obtained from the growth of *Ashbya*. A sample of Eimer and Amend flake agar contained about one-twentieth as much.

Effect of biotin or agar extract in liquid cultures. That a biotin deficiency is responsible for the failure of the (V) strain of *F. avenaceum* to grow in liquid culture lacking organic substances other than sugar and that its biotin content is primarily but not entirely responsible for the beneficial effect of agar was further demonstrated by the following:

The (V) strain was grown in 25 ml. quantities of solution 2, solution 2 plus 0.01 microgram of biotin per flask, solution 3, and solution 3 plus 0.01 microgram of biotin per flask. A suspension of spores from a culture on solution 2 solidified with 1.5 per cent purified Difco agar plus extract equivalent to 15 per cent agar was used as inoculum. The experiment was performed in triplicate. The spores germinated but very little mycelium developed in the solutions without biotin. Considerable growth occurred in the solutions with biotin; the growth in solution 3 was somewhat better than in solution 2.

TABLE 4

Growth of F. avenaceum in solutions supplemented with pure biotin, with agar extract, or with pure biotin and mineral supplements. Age 7 days.

Additions to 25 ml. of solution 3	Amt. biotin in agar extract det'd by growth of *Ashbya* microgram	Amt. biotin in agar extract det'd by du Vigneaud microgram	Av. dry wt. mycelium per culture mg.
None	......	......	No growth
0.001 microgram biotin	......	......	1.4
0.005 microgram biotin	......	......	3.6
0.01 microgram biotin	......	......	6.7
0.05 microgram biotin	......	......	16.7
0.1 microgram biotin	......	......	21.7
0.0125 ml. agar extract	0.00119	0.0005	10.6
0.0250 ml. agar extract	0.00238	0.0010	11.8
0.0625 ml. agar extract	0.00595	0.0025	17.9
0.125 ml. agar extract	0.0119	0.0051	24.9
0.25 ml. agar extract	0.0238	0.0103	29.1
0.5 ml. agar extract	0.0476	0.0205	35.4
1.25 ml. agar extract	0.1190	0.0513	53.1
0.1 microgram biotin and mineral supplements	......	......	22.6

In a second experiment various amounts of biotin or agar extract (table 4) were added to 25 ml. quantities of solution 3 and the cultures inoculated with a suspension of spores as before. To one set of cultures containing 0.1 microgram of biotin per flask the following mineral supplements were added per liter: 0.027 p.p.m. B, 0.106 p.p.m. Cu, 0.800 p.p.m. Fe, 0.053 p.p.m. Ga, 0.053 p.p.m. Mn, 0.053 p.p.m. Mo, 0.479 p.p.m. Zn. The experiment was performed in quadruplicate. Dry weights were determined after 7 days incubation at 25° C.

The spores germinated but no weighable mycelium was obtained in the cultures with no organic material except dextrose. In the flasks containing 0.001 microgram of biotin 1.4 mg. of mycelium was secured, and the amount of growth increased with the quantity of biotin supplied up to 21.7 mg. with 0.1 microgram of biotin. The addition of the mineral supplements to cultures containing 0.1 microgram of biotin made no significant improvement. This suggests that mineral supplements were not responsible for the superiority of agar extract as compared to pure biotin. The addition of 0.0125 ml. of agar extract (1.25 mg. dry matter) per flask permitted 10.6 mg. of mycelium to develop and the amount of growth increased with the amount of agar extract up to 53.1 mg. of mycelium with 1.25 ml. of agar extract per flask (table 4).

In the second column of table 4 the amount of biotin supplied by the agar extract per culture is given as calculated from the determinations in table 3, and in the fourth column as determined by du Vigneaud. It is evident that growth with the agar extract was greater than would be expected from its biotin content. For example, a yield of 17.9 mg. mycelium was obtained with 0.00595 microgram of biotin in the agar extract, while the yield with 0.005 microgram of pure biotin was but 3.6 mg.; 53.1 mg. of mycelium were obtained with 0.119 microgram of biotin in the agar extract while 0.1 microgram of pure biotin gave 21.7 mg.

Effect of Ca and Dr fractions. That other growth substances than biotin affect the growth of *F. avenaceum* is further supported by the action of two fractions obtained from potato extract as described earlier (17). The Ca fraction in the amount used was quite beneficial, the Dr fraction was ineffective and combined they gave greater growth than either alone and as great as or greater than the most favorable amount of agar extract (table 1). The Ca fraction probably contained biotin as well as other growth substances, since it is a charcoal eluate from an extract of potato tubers. The Dr fraction contained little or no biotin, since it is the filtrate from the charcoal-treated potato extract. It is of some interest to contrast the effect of these fractions on *F. avenaceum* and on *Phycomyces Blakesleeanus.* The latter organism was affected by the Dr fraction to a considerably greater degree than by the Ca fraction (17).

Mutation of strain (V) and biotin deficiency. In the course of our experiments it was observed that an inoculation from a subculture of strain (V) grew satisfactorily in solution 2 although inoculations from the parent culture made earlier into the same medium had not grown. This variant from strain (V) grew also on solution 2 solidified with purified Difco agar; on solution 2 solidified with 1.5 per cent Difco agar it grew more rapidly than strain (V) and had a less tufted and more uniform cottony white aerial mycelium. Both produced considerable reddish pigment. A second variant appeared which grew on purified agar but was without pigment.

It was noted also that in one or two tubes of a half-dozen containing solution 2 and 1.5 per cent purified agar vigorous growth had occurred after a month, though for two weeks the inoculum had shown little growth and in the balance of the tubes the development was still slight after a month.

Furthermore, although on some media, for example those to which extract equivalent to 5 or 15 per cent agar had been added, the growth was uniform, on other media considerable local differences in color or character of mycelium appeared as the cultures aged.

The following explanations for these observations were considered.

The original culture of strain (V) might have been mixed, containing an organism with a biotin deficiency and others which were self-sufficient so far as that growth substance was concerned. This did not seem probable because of the difficulty of conceiving that the self-sufficient strains in such a mixture lay dormant on a biotin deficient medium for a week or more and then sprang into active growth, as occurred in some instances in old tubes containing solution 2 and purified agar. It was thought unreasonable also to expect several inoculations made from a culture of strain (V) to fail to grow in solution 2, which would mean that only the biotin-deficient element of the mixture had been transferred, while inoculations made from a subculture of the parent culture grew in the biotin-deficient medium.

It might be suggested that strain (V) became contaminated in the course of an experiment. This was considered unlikely because no other *Fusaria* than the three strains mentioned were in culture in the laboratory and most of the variants isolated from strain (V) were clearly different from strains (M) and (N) as well as (V).

It was thought also that strain (V) might possess a limited ability to synthesize biotin and that after two or three weeks on a biotin-deficient medium sufficient biotin might have been accumulated in the mycelium used as inoculum to permit growth to occur. However, the rapidity of growth once it started and the fact that subcultures from this growth were morphologically different from strain (V) made such an explanation untenable.

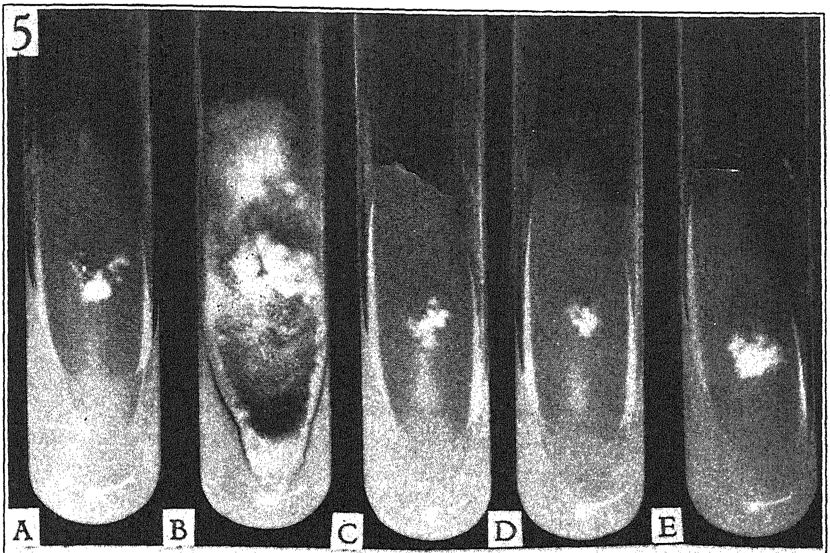
The fourth explanation considered was that strain (V) was unstable and produced saltations, dissociations, or mutations some of which were self-sufficient for biotin. Mutation is a well-known and common phenomenon in the *Fusaria*. Burkholder (3), Brown (2), Leonian (9), Sahai Vasudeva (19), Snyder (20), Orton (12), and others have contributed observations on its occurrence. The validity of this hypothesis was tested as follows:

Mono-conidial cultures. Two single-spore isolations from strain (V) were made. For this purpose a macro-conidium from a culture on solution 2 solidified with 1.5 per cent purified agar and containing extract equivalent to 15 per cent agar was used. Each mono-conidial isolation was grown on a thiamin-peptone agar. At intervals bits of mycelium were removed from each isolation and transferred to 5 slopes of solution 2 containing 1.5 per cent purified agar. The following results were obtained.

Five transfers from each monoconidial isolation were made to solution 2 containing 1.5 per cent purified agar when the cultures were two days old. These transfers grew slowly and by the end of 12 days the raised convoluted colonies were all of about the same size and averaged 1 cm. in diameter. By the end of 19 days three of the ten transfers showed evidence of a spreading surface growth and several were surmounted by white tufts but no colony had completely covered the agar slope. After a month eight of the ten had nearly covered the surface of the slope, the new growth consisting of reddish mycelium closely appressed to the agar. Transfers made from this later growth grew well on purified agar, indicating that a strain or strains self-sufficient for biotin had developed from the original biotin-deficient strain. Similar transfers were made from the monoconidial isolations when they were 4, 7, 9, 14, 21, and 28 days old, making a total of 70 transfers to purified agar from the monoconidial cultures on thiamin-peptone agar. One only of these 70 subcultures grew rapidly within the first week after transfer, which suggests that a mutation had occurred on the thiamin-peptone agar and had been transferred to the purified agar. Thirty-five of the remaining 69 cultures on the purified agar grew slowly for one, two, or three weeks and then grew rapidly, covering the surface of the agar slopes (fig. 5). Transfers to purified agar from the rapidly spreading mycelium of these cultures grew well, showing that mutation to a type capable of growing on a biotin-deficient medium had occurred (fig. 6). Transfers from the convoluted colonies which were growing slowly on the purified agar to the same medium either grew slowly or failed to grow. It is possible that all 69 of the transfers would have developed biotin-sufficient mutations if they had been observed for a longer period of time.

It is not possible to say that mutations occurred more frequently on the biotin-deficient medium, although the data cited above would seem to support that assumption. It should be remembered that on the biotin-deficient medium a mutation of strain (V) toward biotin sufficiency became evident because it spread over most of the agar surface. On a medium containing biotin a similar mutation would be overlooked and found by accident only. It is obvious that many questions on the type of mutation of *F. avenaceum* observed here remain to be studied.

The slow growth of strain (V) on the purified agar indicates either that biotin was not completely removed from the agar by the method of extraction employed or that the organism is able to synthesize a small and insuffi-



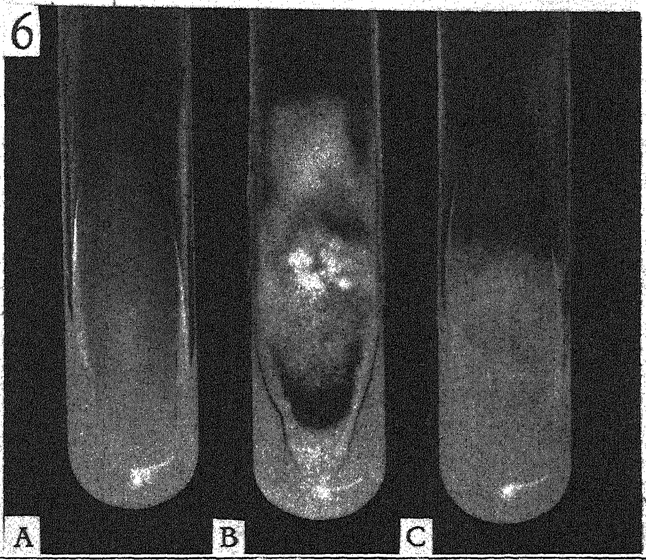


FIG. 5. Mutation of strain (V) to biotin-sufficient form. Five transfers from 9-day-old mono-conidial culture of strain (V) on thiamin-peptone agar to solution 2 plus purified agar. Age of transfers 12 days. Note that 4 of transfers have grown slowly and one has developed spreading growth over surface of agar. Transfer B resembled A, C, D, and E for first 7 days. FIG. 6. Cultures of strain (V) on solution 2 plus purified agar. B, mutating culture shown in figure 5. A, transfer from culture B when it was 2 days old before mutation developed; C, transfer from culture B when it was 9 days old after mutation had developed. Age of culture A was 7 days and of C was 3 days.

cient amount of the growth substance. The failure of the spores to do more than germinate in a liquid culture lacking biotin suggests that the former interpretation is perhaps correct.

DISCUSSION

Biotin deficiencies have been reported for a number of filamentous fungi including *Nematospora gossypii* (*Ashbya gossypii*) and *Lophodermium pinastri* (8), *Melanconium betulinum* and *Hypoxylon pruinatum* (4), *Marasmius androsaceus* and *Marasmius perforans* (11), *Melanospora destruens, Podospora curvula, Sordaria fimicola,* and *Sordaria sp.* (6). The work reported in this paper adds at least one strain of *Fusarium avenaceum* to this list.

Differences in growth substance deficiencies for strains of a given fungus also have been reported. Lindeberg (11) found one strain of *Marasmius perforans* to be biotin deficient while other strains of the same organism were autotrophic for that substance. Hawker (6) found some strains of *Melanospora destruens* to be biotin autotrophic while others were biotin deficient. Houston (7) reported one strain of *Corticium vagum* to require the addition of thiamin to the medium while others grew satisfactorily without its addition.

Mutations in the fungi resulting in a change in growth substance deficiencies are not unexpected but have not hitherto been reported, though Leonian and Lily (10) suspected the occurrence of such mutations in some of their experiments. It seems very probable that fungi differ considerably in their stability with regard to growth substance deficiencies. We have cultivated *Phycomyces Blakesleeanus* for over 6 years and have never observed a change which permitted it to grow in the absence of thiamin. Williams (22) states that strains of *Saccharomyces cereviseae* have been cultivated in his laboratory for more than 15 years without changing their characteristics. However, the demonstration that mutations involving changes in the ability to synthesize growth substances do occur is of importance in the use of microorganisms for bio-assays, the study of the growth-substance deficiencies of microorganisms, and the investigation of the adaptive production of enzymes.

The development from the biotin-deficient (V) strain of *Fusarium avenaceum* of mutations which were autotrophic for that growth substance raises the question as to whether the (M) and (N) strains which also were biotin autotrophic may not have been derived by mutation from a biotin-deficient strain similar to the (V) strain. It is of interest to record that in our experiments we obtained from the (V) strain a biotin-autotrophic variant which closely resembled in general appearance, habit of growth, and spore form the (M) and (N) strains.

The presence of biotin in agar was previously reported by Allison and Hoover (1), Hawker (6), and Robbins (16). To find in some samples of agar as large an amount as reported here is somewhat surprising and emphasizes again the necessity of regarding agar as far more than a convenient means of solidifying a liquid medium.

Although the favorable effect of agar on the growth of *F. avenaceum* can be ascribed primarily to its biotin content our observations show that Difco agar is more effective than can be accounted for by its biotin content. It seems probable that this is due to the presence in agar of unidentified growth substances, since the addition of a readily available source of organic nitrogen (asparagine) or of mineral supplements to purified agar containing biotin did not improve the growth of *Fusarium*. One of the authors (16) has reported unidentified growth substances in agar which affect the development of *Phycomyces*, and these may be responsible also for that portion of the effect of agar on *Fusarium* which cannot be accounted for by the biotin in the agar.

SUMMARY

A strain of *F. avenaceum* did not grow in a mineral-sugar solution but grew in the same solution solidified with agar. The beneficial effect of the agar was primarily due to its biotin content. Some samples of agar were found to contain as much as 0.1 microgram of biotin per gram. The strain of *F. avenaceum* studied was favorably affected by 0.001 microgram of pure biotin methyl-ester, but greater effects were obtained with larger amounts of biotin. Extraction of agar with aqueous pyridine removed all or almost all of the biotin. Agar extract had a greater beneficial effect than could be accounted for by its biotin content. This may be the result of unidentified growth substances which are probably not pyridoxine, pantothenic acid, thiamin, nicotinamide, para-aminobenzoic acid, pimelic acid, i-inositol, riboflavine, glutamine, vitamin K_1, or ascorbic acid. Mutations which grew on a biotin-deficient medium were observed.

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AND
DEPARTMENT OF BOTANY, COLUMBIA UNIVERSITY
NEW YORK

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RED-BLOTCH OF HIPPEASTRUM

THOMAS LASKARIS AND B. O. DODGE

(WITH FIVE FIGURES)[1]

As a rule species of *Hippeastrum* are rarely affected by any serious fungous disease. In March, 1941, Mr. E. Delafield of Riverdale-on-the-Hudson called our attention to a disease which was causing extensive damage to his collection of *Hippeastrum* (spring-flowering amaryllis). The plants, grown from bulbs purchased from Florida, showed various stages of a disease which affected the flower scapes, leaves, and bulb scales. A few weeks later similar symptoms were noted in a shipment of *Hippeastrum* obtained from Florida and grown at the New York Botanical Garden. Microscopic examination of diseased tissue revealed the presence of brown pycnidia of a fungus identified as *Stagonospora curtisii*, which was also readily obtained in pure culture from plantings of sterilized diseased tissue. The spores of this species are classed under the hyalophragmae, but one- and two-celled spores are often very common.

In this country *Stagonospora curtisii* has been described as a rather mild pathogen of amaryllis, forming conspicuous but rather small bright red spots which blemish and occasionally deform the leaves, scapes, and flowers of otherwise perfect plants. Leaf scorch, an important disease of *Narcissus*, is also caused by *S. curtisii*.

We were unable to find a description of a severe form of this disease on *Hippeastrum* such as has come under our observation. The symptoms which characterized the disease were the severe stunting and distortion of the flower stalks. Affected stalks did not make a normal upright growth but grew at an angle, some almost at a right angle to the main axis of the plants (fig. 1). This type of injury was found associated with cankers that had developed on only one side of the stalks. The fact that the cankered side of the young stalks is unable to grow as rapidly as the uninjured side doubtless accounts for the curvature in the affected stalks. A similar curvature of the stalk may result from injury at the point of emergence, a rough red bruise which may be confused with the canker caused by *Stagonospora*. The young flower shoots of *Hippeastrum* are very tightly compressed by the enveloping bulb scales, and, as they emerge, sand or other foreign particles caught between a stalk and the bulb scales may cause a scouring or roughening of the epidermis and the tissue beneath; the resultant unequal growth would cause the curvature and stunting shown in figure 5. It is quite probable that such injuries provide a favorable point of entry for *Stagonospora curtisii*, which may be present on the bulb scales. The fungus can attack the bulb

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[1] Publication of the figures was assisted by the Lucien M. Underwood Memorial Fund.

scales and probably lives through the dormant period by this means. Some cankers are well developed by the time that the young shoot has emerged, which indicates that the fungus has been at work for a considerable period of time. The degree of the curvature of the stalk appears to be closely correlated with the size of the canker.

The cankers themselves are very striking in appearance. Young cankers are bright red or vermillion in color, but as they enlarge and elongate the center of the lesion becomes soft, brown and sunken. In still later stages a mat of the white or brownish gray mycelium of the causal organism develops in the center, while the borders of the canker retain the pronounced red color (fig. 1). Cankers have been observed several inches in length and from one-quarter to one-half inch in diameter (fig. 3). Elongated red spots on the leaves (fig. 4) and red streaks on the scapes, similar to those usually described as characteristic of this disease, were also observed. The flower buds borne on cankered stalks may open normally and persist in good condition for as long a period as those of healthy plants.

The pathogenicity of the fungus which was isolated has been established by inoculating amaryllis leaves with its mycelium and spores. Freshly wounded and sound leaves were inoculated with mycelium from cultures on potato-dextrose agar. Leaves of the control plants were wounded or left unwounded, and sterilized agar was placed on the injured as well as on the uninjured parts. Bell jars were placed over all the plants and removed after 48 hours. Within twenty-four hours distinct watersoaked areas were evident around the wounds. These spread rapidly, and eventually involved the greater part of the leaves. The centers of the lesions became necrotic and reddish brown, while the tissues around the necrotic regions were yellowish red in color. Similar lesions developed on leaves that were inoculated without wounding. Three weeks after inoculation the inoculated leaves were dead and dry, while no disease appeared on the controls. Repetition of these experiments with leaves cut from healthy plants and inoculated in moist chambers gave similar results.

Plants were also sprayed with a suspension of ground mycelium and pycnidia of the fungus. Bell jars were placed over inoculated and uninoculated plants and removed after 48 hours. Symptoms of infection of the

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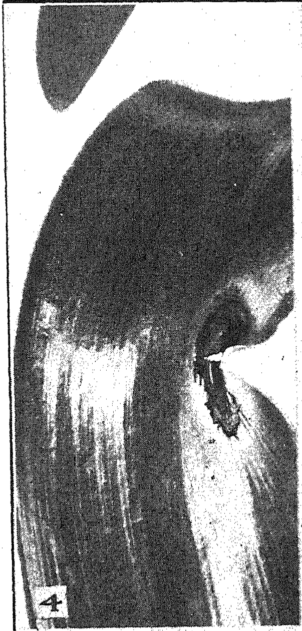
Explanation of figures 1–5.

FIG. 1. Red blotch canker at the base of a flower stalk which has been stunted and bent at right angles. Several small reddish spot infections may be seen on the flower stalk above the canker. FIG. 2. Canker at the base of flower stalk artificially infected. Mat of mycelium plainly visible on the surface. The stalk was considerably bent sidewise. FIG. 3. Canker on a flower stalk from Mr. Delafield's collection. A mass of mycelium covered some of the surface of the canker. FIG. 4. Leaf blotch which induces kinking of the leaf at the point of infection. FIG. 5. Bending and stunting of the flower stalk primarily due to mechanical injury to the epidermis and underlying tissue of the stalk as it emerges from the bulb.



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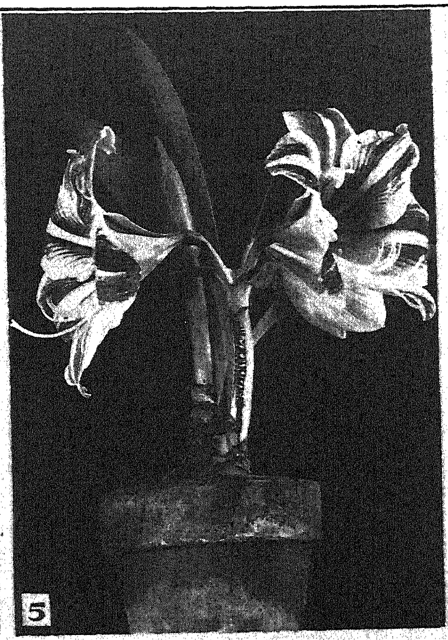

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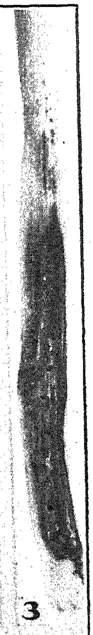

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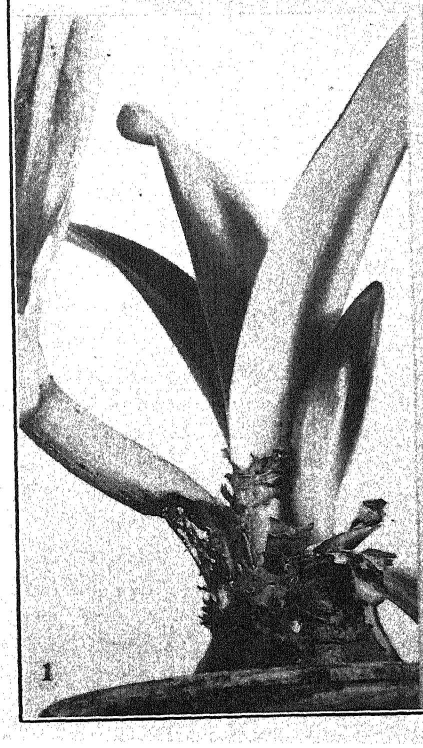

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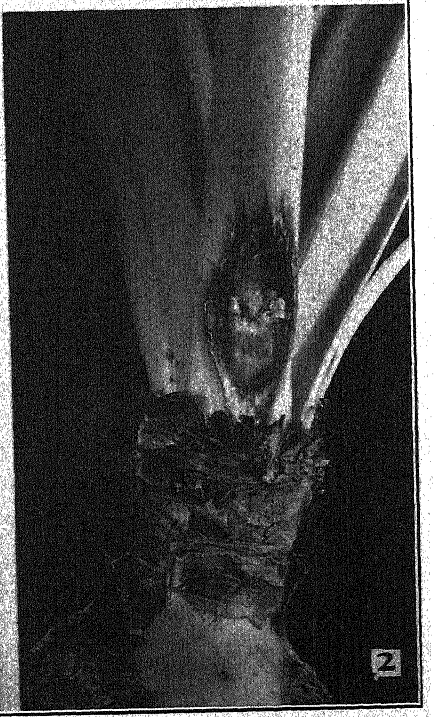

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inoculated plants appeared in less than a week. Hundreds of minute red spots or streaks then developed on the flowers, scape, and leaves. These enlarged during the ensuing weeks and disfigured the plants considerably. On the controls no symptom of disease appeared during the same period.

Since large cankers did not develop on any of the plants so inoculated, another experiment was made. A young flower shoot that was just emerging was injured at its base by scraping the epidermis lightly with a sterile scalpel, and a small square of an actively growing agar culture of *S. curtisii* was placed on the wounded surface. Figure 2 shows the canker that developed on this shoot after two weeks. As the canker increased in size, the stalk ceased growing in an upright direction and became bent at an angle away from the main body of the plant, thus producing the effect observed on plants naturally infected with canker.

The following genera of the Amaryllidaceae are known to be susceptible to *Stagonospora curtisii: Amaryllis, Chlidanthus, Crinum, Galanthus, Hippeastrum, Hymenocallis, Leucojum, Lycoris, Narcissus, Pancratium, Sternbergia, Sprekelia, Zephyranthes,* and *Eucharis*. Smith,[1] who studied the host range of this fungus extensively, was unable to obtain infection when he inoculated species of a number of Liliaceae, including *Hemerocallis aurantiaca*. A number of *H. fulva* seedlings inoculated by us under conditions favorable to infection failed to become diseased.

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[1] C. O. Smith. Inoculations of *Stagonospora curtisii* on the Amaryllidaceae in California. Phytopathology **25**: 262–267. 1935.

DESCRIPTIONS OF TROPICAL RUSTS—IV[1]

George B. Cummins

(WITH FOUR FIGURES)

Phakopsora cherimoliae (Lagerh.) Cummins, comb. nov. (*Uredo cherimoliae* Lagerh., Bull. Soc. Myc. Fr. **11**: 215. 1895; *Uredo cupulata* Ellis & Ev., Field Mus. Publ. Bot. **2**: 16. 1900; *Physopella cherimoliae* Arth., Résult. Sci. Congr. Bot. Vienne 338. 1906.)

Telia developing in the base of old uredia or usually separately in hypophyllous, subepidermal, reddish brown crusts 0.1–1 mm. in diameter and 3–6 spores in thickness, the outer layers of spores golden- or light chestnut-brown, the basal layers paler; teliospores cubical, oblong or oblong-ellipsoid, 7–13 × 13–23 μ; wall 1–2 μ thick or slightly thicker apically in the outermost spores.

On *Anona cherimolia*, GUATEMALA: Moran, Feb. 11, 1905, *W. A. Kellerman 5463*.

This rust is not uncommon, in the uredial stage, in tropical regions of the Americas from Florida to Ecuador.

ANGIOPSORA COMPRESSA Mains, Mycologia **26**: 129. 1934. (*Uredo paspalicola* P. Henn., Hedwigia **44**: 57. 1905; *Uredo stevensiana* Arth., Mycologia **7**: 326. 1915; *Puccinia compressa* Arth. & Holw.; Arthur, Proc. Am. Phil. Soc. **64**: 157. 1925; not *Puccinia compressa* Diet., Ann. Myc. **5**: 245. 1907; *P. paspalicola* Arth., Manual Rusts U. S. & Canada p. 127. 1934, in part.)

In a previous paper (Bull. Torrey Club **67**: 607. 1940) this rust was recorded for the first time in North America from Guatemala. It was stated then that it might have been previously collected but referred to *Puccinia paspalicola* (P. Henn.) Arth. (*P. tubulosa* (Pat. & Gaill.) Arth.). Subsequent examination of the rusts of *Paspalum* in the Arthur Herbarium proved that *A. compressa* is of common occurrence in tropical regions of the Americas but had been confused with various species. The species usually occurs in the uredial stage only, but I have seen telial specimens from Bolivia, Guatemala, and Puerto Rico.

As a result of these studies the above synonymy is presented. The known hosts and distribution are as follows: *Axonopus compressus:* Guatemala, Louisiana (U.S.A.), Puerto Rico; *Paspalum conjugatum:* Brazil, Cuba, Florida (U.S.A.), Guatemala, Dominican Republic, Panama, Peru, Puerto Rico, Venezuela; *P. decumbens:* Venezuela; *P. distichophyllum:* Brazil; *P. elongatum:* Bolivia; *P. fasciculatum:* Guatemala; *P. humboldtianum:* Bolivia, Guatemala, Mexico, Venezuela; *P. paniculatum:* Puerto Rico, Venezuela; *P. plicatulum:* Brazil, British Honduras, Cuba, Puerto Rico; *P. trachycauleon:* Venezuela; *P. virgatum:* Bolivia; *P.* sp.: Guatemala, Texas (U.S.A.).

Hemileia oxyanthi Cummins, sp. nov. Urediis hypophyllis, partes minores foliorum dense obtegentibus, pallide flavidis, minutissimis, per

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[1] Contribution from the Department of Botany, Purdue University Agricultural Experiment Station, Lafayette, Indiana.

The third article of this series was published in Bull. Torrey Club **67**: 607–613. 1940.

stomata erumpentibus; urediosporis in apice hypharum fasciculatim erumpentium ortis, obovoideis, triangularis vel ellipsoideis, 18–23 × 24–29 μ; membranis hyalinis vel dilute flavidis, 1.5–2.5 μ cr., parte superiore moderate aculeatis, inferiore minuteque echinulatis vel fere levibus. Teliis adhuc ignotis.

On *Oxyanthus speciosus*, UGANDA: Entebbe Road, August 1940, *C. G. Hansford 2784.* TYPE specimen deposited in the Arthur Herbarium, the Herbarium of the Imperial Mycological Institute, and the Mycological Collections of the Bureau of Plant Industry, United States Department of Agriculture.

The sori usually occur in small, dense, interveinal groups but are occasionally somewhat more scattered. This specimen was made available through the courtesy of Dr. John A. Stevenson of the Bureau of Plant Industry.

Puccinia aspiliae-latifoliae Cummins, comb. nov. (*Uredo aspiliae-latifoliae* Cummins, Bull. Torrey Club **68**: 47. 1941.)

Telia not seen; teliospores in the uredia clavate or oblong-ellipsoid, rounded above, narrowed below, moderately constricted at the septum, 16–22 × (34–) 38–52 μ; wall 1–1.5 μ thick at sides, thickened to 3–5 μ at apex, yellowish or pale golden, smooth; pore apical in upper cell, next the septum in the lower cell; pedicel shorter than the spore, hyaline or yellowish, thin-walled. The teliospores germinate at once.

On *Aspilia latifolia*, SIERRA LEONE: Sefadu, Dec. 6, 1938, *F. C. Deighton 1658.*

Aside from characteristics mentioned in the description (*l.c.*) of the uredia this rust also differs from other species described on *Aspilia* because of narrower teliospores whose apical wall is only moderately thickened.

The specimen was made available through the courtesy of Dr. G. R. Bisby of the Imperial Mycological Institute.

Puccinia henryae Cummins, sp. nov. (Fig. 1.) Uredia hypophylla, sparsa, rotundata, 0.1–0.3 mm. diam., pulverulenta, obscure cinnamomeo-brunnea; urediosporae globoideae vel late ellipsoideae, 25–32 × 28–36 μ; membrana cinnamomeo-brunnea, 2.5–3 μ cr., moderate echinulata; poris germ. 2, aequatorialibus. Telia hypophylla, sparsa vel plus minusve aggregata, rotundata, 0.3–0.5 mm. diam., pulvinata, flavida; teliosporae clavatae vel oblongo-clavatae, ad apicem rotundatae, deorsum attenuatae, medio leniter constrictae, 18–25 × 40–50 μ; membrana 1.5 μ cr., ad apicem 5–8 μ cr., flavidula vel fere hyalina, levi; poro superiore apicali, inferiore juxta septum sito; pedicello persistenti, hyalino, sporam aequante. Statim germ.

On *Henrya imbricans*, GUATEMALA: Laguna (Lake Amatitlan), Dept. Amatitlan, Jan. 20, 1906, *W. A. Kellerman 5390.* TYPE deposited in the Arthur Herbarium.

This appears to be the first rust recorded on the genus *Henrya* and there is no species of *Puccinia* on other genera of the Acanthaceae to which it can be referred.

The identity of the host was recently verified by E. C. Leonard of the U. S. National Museum.

Puccinia opipara Cummins, sp. nov. (Fig. 2.) Uredia hypophylla, sparsa, ovoidea, 0.1–0.4 mm. longa, flavida; urediosporae late ellipsoideae vel ellipsoideae, 25–31 × 31–40 (–43) μ; membrana 1–1.5 μ cr., pallide flavida

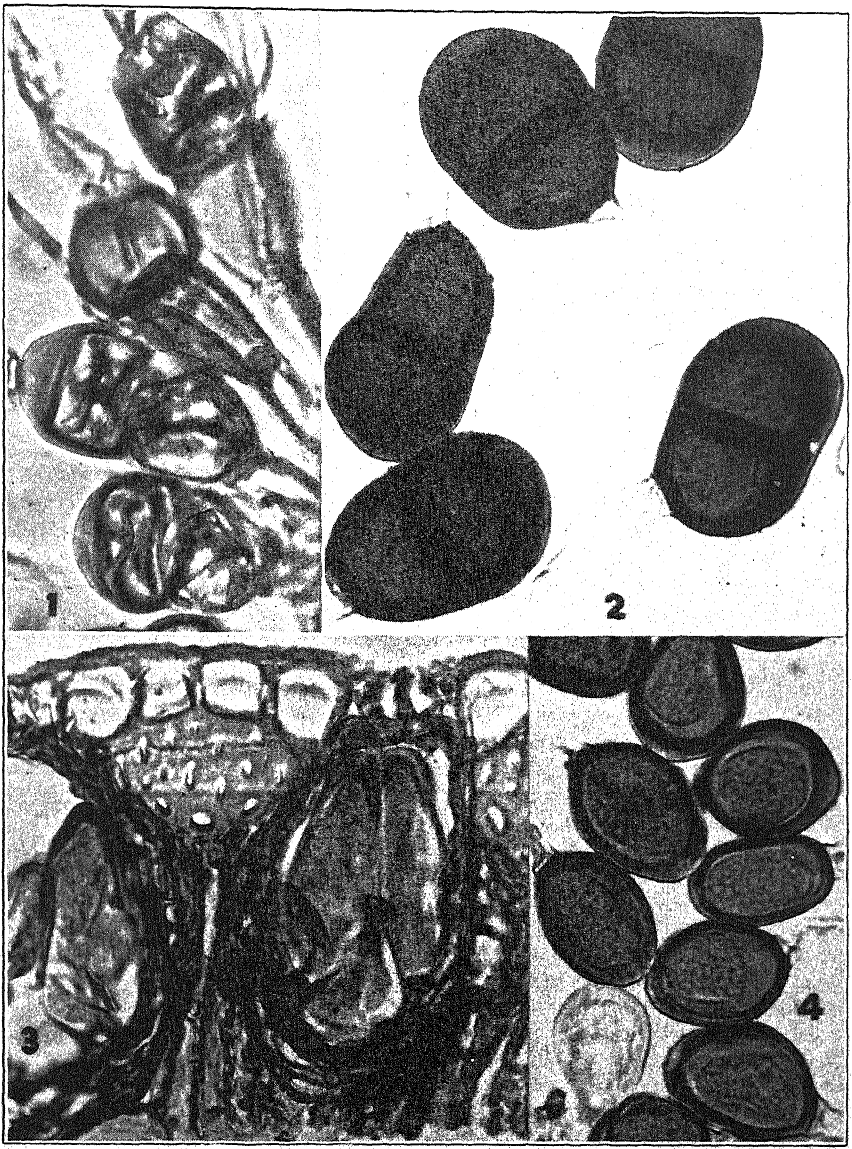

FIG. 1. Teliospores of *Puccinia henryae*, two of which have germinated and collapsed. (From type.) ×800. FIG. 2. Teliospores of *Puccinia opipara*. The wall is rather opaque and has a peculiar smoky tint. (From type.) ×800. FIG. 3. Photograph of a freehand, unstained section of the telia of *Uromyces bermudianus*, showing the substomatal position and thin peripheral layer of brownish, peridium-like hyphae. These sori are individual and not locules in a compound telium. (From type.) ×800. FIG. 4. Teliospores of *Uromyces cruckshanksiae*. The spores actually are faintly and longitudinally striate. (From type.) ×800.

vel fere hyalina, moderate echinulata; poris germ. plus minusve obscuris, 3 vel 4, aequatorialibus. Telia hypophylla, sparsa, pulvinata, rotundata vel oblonga, 0.3–0.8 mm. longa, atro-brunnea; teliosporae ellipsoideae, utrinque rotundatae vel deorsum leniter attenuatae, medio non vel vix constrictae, 23–28 (–31) × 33–44 µ; membrana 2–3 µ cr., ad apicem 4–7 µ, obscure castaneo-brunnea, levi; poro superiore apicali, inferiore juxta septum sito; pedicello sporam aequante vel longiore, pallide flavido, persistenti.

On *Oplismenus minarum*, BOLIVIA: Sorata, Apr. 17, 1920, *E.W.D. & Mary M. Holway 541* (TYPE); Coroico, Prov. de Nor Yungas, June 14, 1920, *E.W.D. & Mary M. Holway* ex *735*. Type deposited in the Arthur Herbarium.

The specimen taken as the type was originally reported by Arthur (Proc. Am. Phil. Soc. **64**: 169. 1925) as *Puccinia inclita* Arth. but was later issued in Reliquiae Holwayanae no. 82 as *Puccinia levis* (Sacc. & Bizz.) Magn. The second specimen cited was separated from Holway's no. 735 which Arthur (*l.c.* p. 176.) reported correctly as *P. levis*.

P. opipara is unlike previously described rusts on *Oplismenus*. Its teliospores have a general resemblance to those of *P. inclita* but are considerably darker in color, are more opaque and have a peculiar smoky tint. The urediospores of *P. inclita* are significantly smaller (22–26 × 24–32 µ).

Uromyces bermudianus Cummins, sp. nov. (Fig. 3.) Uredia culmicola, sparsa, ovoidea vel linearibus, 0.4–1.5 mm. longa, bullata, epidermide elevata conspicue, cinnamomeo-brunnea; urediosporae ellipsoideae vel oblongo-ellipsoideae, 16–20 (–22) × (26–) 28–35 (–37) µ; membrana pallide cinnamomeo- vel aureo-brunnea, minuteque echinulata; poris germ. 4 vel 5, aequatorialibus. Telia circum uredia denseque aggregata, subepidermalia, indehiscentibus, rotundata, 40–60 × 55–80 µ; teliosporae oblongae vel cylindraceae, 14–20 × (30–) 35–50 (–55) µ; membrana 1 µ cr., ad apicem 2–4 µ cr., aureo-brunnea vel ad basim flavidula, levi; pedicello persistenti, brevi, 5–10 µ longo, brunneolo.

On *Cyperus paniculatus*, BERMUDA: Paget Marsh, Nov. 28, 1940, *F. J. Seaver & J. M. Waterston 351*. TYPE deposited in the Arthur Herbarium and the Herbarium of the New York Botanical Garden.

Uromyces bermudianus is quite unlike any previously described species of *Uromyces* on *Cyperus* because of the indehiscent, substomatal, minute telia. The telia are individual, i.e. not locules separated by stromatoid paraphyses, and have only a thin peripheral layer of brown peridium-like cells. Macroscopically, however, they are greyish black and simulate multiloculate telia because they are so uniformly distributed about the uredia. Through confluence the telial spots may become continuous over areas several millimeters in length.

While there is no similar *Cyperus* rust there is a morphologically related species, *U. americanus* Speg., on *Scirpus* (see Cummins, Mycologia **27**: 611. 1935). *U. americanus* has similar sori but with the teliospores somewhat and the urediospores much longer.

Uromyces cruckshanksiae Cummins & Bonar, sp. nov. (Fig. 4.) Pycnia aequaliter sparsa, subepidermalia, amphigena, globoidea, 130–160 µ diam., paraphysata. Aecia plerumque hypophylla, ubique aequaliter denseque distributa, cupulata, 2.5–4 mm. diam., peridio lacerato vel plus minusve recurvato, cellulis peridii firme conjunctis, oblongis, cuboideis vel polyhedricis, 16–25 × 23–36 μ, pariete interiore verrucoso 2.5–3.5 μ cr., exteriore minuteque striato 6–8 μ cr.; aeciosporae globoideae, ellipsoideae vel oblongae, 17–22 × 19–27 μ; membrana 1–1.5 μ cr., minuteque verrucosa. Uredia non visa; urediosporae globoideae vel late ellipsoideae, 24–33 × 29–38 μ; membrana 2.5–3.5 μ cr., hyalina vel pallide flavida, moderate echinulata; poris germ. obscuris. Telia amphigena, ubique aequaliter denseque distributa, pulverulenta, castaneo-brunnea, rotundata, 0.2–0.4 mm. diam. vel confluentibus; teliosporae ellipsoideae, ovoideae vel oblongo-ellipsoideae, 17–23 × 23–30 (–34) μ; membrana 1.5–2.5 μ cr., ad apicem 3–6 μ cr., obscure cinnamomeo- vel castaneo-brunnea, minuteque longitudinaliter striata vel sublevibus; pedicello hyalino, brevi, fragili.

On *Cruckshanksia bustillosi*, CHILE: Prov. Coquimbo, Dept. Illapel, La Vega Escondida, three hours by horse east of Cuncumen, Dec. 20, 1938, *J. L. Morrison 16963;* on *C. palma*, same locality and date, *J. L. Morrison 16959* (TYPE). Type deposited in the Arthur Herbarium and the Herbarium of the University of California.

Notes made by the collector concerning the effect of this systemic rust on *C. bustillosi* are as follows: "Perennial herb. 0.1 m. fl. pink bracts; lvs. with rust are erect, the others prostrate; fls. with larger deeper colored bracts in rust-infected plants."

Cruckshanksia, a rubiaceous genus of the Chilean Andes, has not been recorded previously as a host for species of the Uredinales nor have species of *Uromyces*, with which *U. cruckshanksiae* can be confused, been described on Rubiaceae.

UREDO ROUPALAE Cumm. (Bull. Torrey Club **64**: 43. 1937) is synonymous with *Uredo mauriae* Syd. and the host is *Mauria glauca* rather than *Roupala veraguensis.*

Aecidium archibaccharidis Cummins, sp. nov. Pycnia plerumque hypophylla, subepidermalia, 90–125 μ diam., paraphysata. Aecia hypophylla, in maculis flavo-brunneis usque ad 1 cm. diam. aggregata, cupulata, 200–250 μ diam., margine recurvato; cellulis peridii firme conjunctis, flavidis, oblongis vel oblongo-ellipsoideis, 20–27 × 40–48 μ; pariete interiore moderate verrucoso 3–4 μ cr., exteriore striato 3–5 μ cr.; aeciosporae globoideae, 18–23 × 18–25 μ; membrana hyalina vel pallide flavida 1 μ cr., ad apicem 7–13 μ, laxe verrucosa, verrucis plus minusve deciduis usque ad 2.5 μ diam.

On *Archibaccharis serratifolia*, GUATEMALA: Mauchen, July 22, 1936, *J. R. Johnston 79* (TYPE), July 18, 1937, *J. R. Johnston 875*. Type deposited in the Arthur Herbarium and the Herbario de la Escuela Nacional Central de Agricultura, Chimaltenango Guatemala.

A. archibaccharidis is characterized by aeciospores with the apical wall much thickened and by the rather large, sparsely distributed and somewhat deciduous warts which form the sculpturing. The only *Baccharis* rust with similar aeciospores is *A. pachycephalum* Diet. but in it the aecia are caulicolous in position and the mycelium is systemic rather than localized.

The host was identified by P. C. Standley of the Field Museum.

Aecidium nairobianum Cummins, sp. nov. Pycnia non visa, verisimiliter nulla. Aecia plerumque hypophylla, ubique aequaliter denseque distributa, cupulata, 175–300 μ diam., margine lacerato, cellulis peridii firme conjunctis, hyalinis, globoideis, ellipsoideis vel polyhedricis, 17–25 × 25–33 μ, pariete interiore valde verrucoso 3–4 μ cr, exteriore punctato-striato 2.5–3 μ cr.;

aeciosporae variabiles late ellipsoideae, ellipsoideae vel oblongae, 13–22 × 21–33 μ; membrana 2 μ cr., hyalina, verruculosa.

On *Lippia asperifolia*, KENYA, Nairobi, June 1934, *J. McDonald.* TYPE deposited in the Arthur Herbarium and the Herbarium of the Imperial Mycological Institute.

Aecidium nairobianum differs from *A. evansii* Doidge, which has been reported on this host, and from other species on *Lippia* because of its systemic habit.

The specimen was made available through the courtesy of Dr. G. R. Bisby of the Imperial Mycological Institute.

THE ARTHUR HERBARIUM
PURDUE UNIVERSITY AGRICULTURAL EXPERIMENT STATION

STUDIES IN THE CRASSULACEAE—II. MEXICAN SEDOIDEAE COLLECTED BY E. K. BALLS IN 1938

ROBERT T. CLAUSEN

(WITH ONE FIGURE)

Through the courtesy of Dr. W. R. Maxon and Mr. C. V. Morton of the United States National Herbarium, it has been my privilege to study a small series of Crassulaceae obtained in east-central Mexico in 1938 by Mr. Edward K. Balls. The collections include specimens representing interesting variations and range extensions, also one new species of *Sedum*. In the discussion, the species are listed alphabetically.

SEDUM DENDROIDEUM Moç et Sessé. MEXICO: Cueva del Negro-Popo, 11200 ft., April 13, 1938, *E.K.B. 4192* (US 1793595). PUEBLA: Tesmalaquilla, Sierra Negra, Mt. Orizaba, 10600 ft., May 9, 1938, *E.K.B. 4470* (US 1793649). TLAXCALA: Manantiales de la Conchia, Mt. Malinche, 12400 ft., Oct. 15, 1938, *E.K.B. 5649* (US 1793885).

Inclusion of previously little known details concerning the altitudinal distribution of the species, the habitat, and flowering time renders these collections interesting and valuable. In the copious notes on the labels, the habitat is given variously as on sheer cliffs of volcanic rock in full sun, in deep shade, in rocks and steep volcanic screes in shade of cliffs or shrubs, and in deep and shaded barrancos, in moist situations, where the stems hang down from the cliffs.

The leaves of these specimens are spathulate-elliptical, blunt at apex and spurred at base, to 3.5 cm. long and 1.5 cm. wide. The largest inflorescence is 13.5 cm. long and 11 cm. wide. The flowers are yellow. In fruit, the carpels are widely spreading.

The species most closely related to *S. dendroideum* is *S. praealtum*. This differs in the pseudopetiolate leaves which are thinner, subacute, and yellow-green. The leaves of *S. dendroideum* are thick and frequently suffused with red along the margins.

SEDUM MORANENSE H.B.K. HIDALGO: Pena Baron, Parque Nacional de Miguel, 11500 ft., Aug. 11, 1938, *E.K.B. 5234* (US 1793796). VERA CRUZ: below Las Vigas, Cofre de Perote, 8600 ft., *E.K.B. 4752* (US 1793705).

This species is known to me from various places in central Mexico from southern Coahuila to Puebla. There are many collections from Hidalgo, but the specimen cited from Las Vigas is apparently the first from the State of Vera Cruz.

SEDUM NAPIFERUM Peyritsch. MEXICO: Mt. Ixtaccihuatl, 13500 ft., July 30, 1939, *E.K.B. 5178* (US 1793790).

This stonecrop has previously been collected only in the vicinity of Toluca. On Ixtaccihuatl the habitat is on rocks and open sandy slopes in moist places where water seeps through the ground. The plants are annuals, 0.5–3 cm. high. The rootstocks are tuberous-fusiform, to 1.5 cm. long, not globose as in *S. minimum* which may be only a phase of the same species. The fresh flowers are white with red centers, but in the dried condition they are mostly yellowish-white, rarely red.

Sedum obcordatum Clausen, sp. nov. Figure 1. Planta (Sectio *Dendrosedum*) glabra, lignosa, caulibus tortuosis, formans tegetes implicatas ad 60 dm. latas; folia obcordata, late rotunda, truncata vel emarginata, cuneata et sessilia, calcarata, ad 2.8 cm. longa; floris in cymis densis; bracteae florales cinereo-virides, similes foliis; sepalae erectae, lineari-oblongae, obtusae, flavae, ad 1.4 cm. longae; petalae erectae, anguste oblongae-lanceolatae, flavae, ad 1.2 cm. longae.

Plant glabrous, woody, with tortuous stems to 16 cm. or more high, forming tangled mats and tufts to 60 dm. across; leaves alternate, succulent, bluish-gray, obcordate, to 2.8 cm. long and 2.3 cm. broad, broadly rounded, truncate or emarginate, cuneate and sessile, spurred, mostly crowded towards the ends of the stems; inflorescence a dense cyme with large oblong

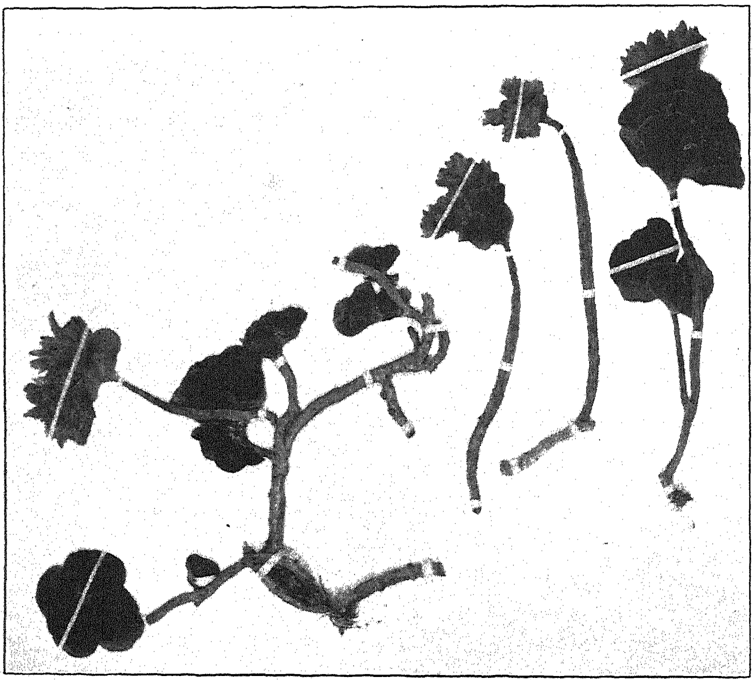

FIG. 1. Type specimens of *Sedum obcordatum* Clausen. Sheet is in the U. S. National Herbarium, no. 1793671. × 4/5.

to linear-lanceolate gray-green bracts subtended below by the proximate foliage leaves; sepals erect, linear-oblong, obtuse, unequal, to 1.4 cm. long, yellow; petals erect, narrowly oblong-lanceolate, submucronate, to 1.2 cm. long, yellow; stamens to 1 cm. long; carpels 9 mm. long, widely spreading in fruit; nectar scales transversely linear, to 1.5 mm. wide and 0.2 mm. long. Hanging from crevices in volcanic cliffs, 12500 ft., Cofre de Perote, State of Vera Cruz, May 24, 1938, *E.K.B. 4600* (TYPE, US 1793671).

This striking plant does not seem referable to any previously described species of Crassulaceae. Although it is here designated as a member of the genus *Sedum*, it in some respects resembles *Pachyphytum* and is thus intermediate between the two genera. Were a large suite of speciments and further data available, there might be basis for founding a new genus. The large floral bracts and the erect sepals and petals are unusual in *Sedum*. Yet the sepals and petals are free to the base and the petals are not appendaged as in *Pachyphytum*. Until further material and information are available, this species seems best placed in the section *Dendrosedum* of *Sedum*, which includes a group of species which are shrubs or subshrubs with yellow flowers and broad, fleshy leaves.

SEDUM OXYPETALUM H.B.K. FEDERAL DISTRICT: Camino de Toluca, 8000 ft., Feb. 10, 1938, *E.K.B. 5590* (US 1793871).

The habitat is indicated as on edges of a steep barranco, among shrubs and herbage. Although the petals are usually described as purplish red, the collector's notes give the color as white or pinkish. *Sedum conzattii* Rose, with puberulent stem and white or purple flowers, is close to this species.

VILLADIA BATESII (Hemsl.) Baehni & Macbride. FEDERAL DISTRICT: Pedregal, 7000 ft., Oct. 4, 1938, *E.K.B. 5595* (US 1793872).

Like Fröderström (1935), I find that the flowers of this species are larger than was indicated by Rose (1905). In the specimen at hand, the corolla is 5–6 mm. long and the calyx 4–5 mm. The habitat is given as sunny exposures in hot crevices in old lava.

Villadia goldmanii (Rose) Clausen, comb. nov. (*Altamiranoa goldmani* Rose, Bull. N. Y. Bot. Gard. 3: 32. 1903). TLAXCALA: Manantiales de la Concha, Mt. Malinche, 12400 ft., Oct. 15, 1938, *E.K.B. 5650* (US 1793886).

To be consistent with the ideas expressed in my recent paper (1940), we must transfer this species to *Villadia*. One of its most striking characters is the tendency to bear scattered rosettes of leaves on the stems. According to the collector's notes, the flowers are pale pink, but Rose described them as pale yellow, tinged with red, orange-colored when dry. The collection cited is from steep sandy volcanic screes.

SUMMARY

Sedum obcordatum (Section *Dendrosedum*) is a new species from the State of Vera Cruz. *Villadia goldmanii* is a new name for the plant known until now as *Altamiranoa goldmani.* Descriptive, habitat and distributional notes are provided for *Sedum dendroideum, S. moranense, S. napiferum, S. oxypetalum* and *Villadia batesii.*

BAILEY HORTORIUM
CORNELL UNIVERSITY
ITHACA, NEW YORK

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NORTH AMERICAN RANUNCULI—II[1]

LYMAN BENSON

8. RANUNCULUS RECURVATUS Poir. in Lam. Encyc. Meth. **6**: 125. 1804. *Ranunculus recurvatus* var. *adpressipilis* Weatherby, Rhodora **31**: 164. 1929. *Ranunculus recurvatus* f. *laevicaulis* Harger ex Weatherby, Rhodora **31**: 164. 1929. *Ranunculus recurvatus* var. *fontinalis* Peattie, Jour. Elisha Mitchell Soc. **44**: 205. 1929. *Ranunculus recurvatus* f. *Hargeri* Weatherby ex Peattie, Jour. Elisha Mitchell Soc. **46**: 155. 1931, as syn. (incorrectly ascribed to Weatherby).

Woods and bottom-land thickets at low elevations; Ottawa, Ontario, and Minneapolis, Minnesota, and eastward to Newfoundland and southward to Oklahoma (Dripping Springs), Louisiana, and Georgia. Coniferous and deciduous forest belts. Late April to June.

Type collections: (1) *R. recurvatus*, "Cette plante croîte en Amérique, dans les environs de New York . . . in herb. Lamarck." (2) Var. *adpressipilis*, "VIRGINIA: Hungry Hollow, alt. 2200 ft., northeast of Marion, Smyth Co., May 24, 1892, Small, TYPE in Grey Herb." This form is remarkable for appressed hairs, which are unicellular. (3) F. *laevicaulis*, "MASSACHUSETTS: by brook, Whately, May 17, 1913, Fernald & Harger, Type in hb. N. E. B. C. (also a mixed sheet in Herb. Gray). (4) Var. *fontinalis*, "Type specimens: In a waterfall, April 9, 1919 (Day). In a waterfall, Melrose Mt., April 3, 1929 (PT. 068). Pearson's Falls, in the water, May 11, 1926 (PT. no. 2188)." Polk County, North Carolina and adjacent South Carolina. (PT. = Peattie.)

9. RANUNCULUS BONGARDI Greene, Erythea **3**: 54. 1895. *Ranunculus occidentalis* Nutt. var. *parviflorus* Torr. Bot. Wilkes Exped. **17**: 214. 1874. *Ranunculus occidentalis* var. *Lyallii* A. Gray, Proc. Am. Acad. **21**: 373. 1886. *Ranunculus tenellus* Nutt. var. *Lyallii* Rob. in A. Gray, Syn. Fl. N. Am. **1**: 33. 1895. *Ranunculus Greenei* Howell, Fl. N. W. Am. **1**: 18. 1897. *Ranunculus Lyallii* Rydb. Mem. N. Y. Bot. Gard. **1**: 166. 1900. *Ranunculus Bongardi Greenei* Piper, Contr. U. S. Nat. Herb. **11**: 275. 1906.

Hispid perennials; stems 2–6 mm. in diameter, hispid with the hairs commonly reddish-brown; radical leaf blades 3–9 cm. long, 4–14 cm. broad, 3-parted, the parts lobed and acutely toothed, appressed-hispidulous; petioles densely hispid, the hairs usually reddish-brown; cauline leaves similar to and usually smaller than the radical; achenes 8–20 or 25 in a globose-hemispherical cluster 3–4 mm. long by 4 mm. in diameter, each achene obovate, 1.8 mm. long, 1.3–1.5 mm. dorsoventrally, 0.8 mm. laterally, smooth or with a trace of reticulation, hispid, the achene beak slender but broad at the base, 2 mm. long, recurved, hooked at the tip.

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[1] The first article in this series, Bull. Torrey Club **68**: 157–172. 1941, includes a key to the species of the section *Chrysanthe* of the subgenus *Euranunculus* and discussion of the first seven species, *Ranunculus acris, R. acriformis, R. repens, R. bulbosus, R. occidentalis, R. californicus* and *R. canus*. The present delimitation of subgenera and sections was published in an article entitled "The North American subdivisions of *Ranunculus*," Am. Jour. Bot. 27 (9): 799–807. 1940.

Shaded and rather moist places 50–1,000 meters or inland up to 2,000 meters elevation; Pacific slope from Kodiak, Alaska, to Humboldt County, California; occasional in the interior as follows: Kootenai District, British Columbia; northeastern and southeastern corners of Washington; Deschutes River and northeastern Oregon; Warner Valley, Mohawk Valley, and the San Bernardino Mountains, California; Idaho, western Montana, and northwestern Wyoming; North Park, Colorado. Northwestern coniferous and yellow pine forests. Late April to July.

The form occasional in the Rocky Mountains and in the Blue Mountains of Washington and Oregon and the Wallowa Mountains of Oregon has hair around only the margin of the achene, and it is perhaps more closely allied to *Ranunculus Bongardi* var. *tenellus.*

Type collections: (1) Var. *parviflorus,* "Plains between Puget Sound and the Cascade Mountains." *Wilkes Expedition.* (2) Var. *Lyallii,* "Lyall's specimens are from Pend Oreille River, in Idaho." (3) *R. Bongardi,* "**Ranunculus Bongardi.** *R. recurvatus,* Bong. Veg. Sitch mainly, not of Poiret." (4) *R. Greenei.* "*R. occidentalis* var. *Lyallii Gray, Proc. Am. Acad. xxi, 373.* . . . Common in open Fir forest, Oregon to British Columbia." Since no specimen is mentioned, *R. Greenei* is considered to have been proposed as a new name for Gray's var. *Lyallii* and to be based upon the same type.

Significant specimens: cf. L. Benson, Am. Jour. Bot. **23**: 30–31. 1936.

9A. RANUNCULUS BONGARDI var. TENELLUS (Nutt.) Greene, Erythea **3**: 54. 1 Ap 1895. *Ranunculus tenellus* Nutt. in Torr. & Gray, Fl. N. Am. **1**: 23. 1838, not Viviani in 1831. *Ranunculus Nelsonii* (DC.) A. Gray, var. *tenellus* A. Gray, Proc. Am. Acad. **8**: 374. 1872. *Ranunculus occidentalis* Nutt. var. *tenellus* A. Gray, Proc. Am. Acad. **21**: 373. 1886. *Ranunculus Nelsonii glabriusculus* Holzinger, Contr. U. S. Nat. Herb. **3**: 210. 23 N 1895. *Ranunculus Douglasii* Howell, Fl. N. W. Am. **1**: 18. March, 1897. *Ranunculus arcuatus* Heller, Bull. Torrey Club **24**: 319. 29 Je 1897. *Ranunculus Bongardi* var. *Douglasii* Davis, Minn. Bot. Studies **2**: 479. 1900.

Sparsely hirsute or glabrous terrestrial annuals or sometimes perhaps perennials; stems 2–4 or 5 mm. in diameter, glabrous or somewhat hirsute with soft white hairs; radical leaf blades 2–5 or rarely 7.5 cm. long, 2–7 or rarely 13 cm. broad, 3-parted and the parts lobed, the ultimate lobes obtuse or sometimes acute, glabrous; petioles glabrous or somewhat hirsute; cauline leaves usually larger than the radical; achenes 5 or 12–30 in a globose-ovoid or hemispherical cluster 4–5 mm. long by 4–5 mm. in diameter, each achene discoid, obovate, or elliptic, 2–2.5 mm. long, 1.7–1.9 mm. dorsoventrally, 0.8 mm. laterally, smooth or minutely reticulate, glabrous, the achene beak 1–1.5 mm. long, 0.3–0.5 mm. broad at the base, recurved and hooked at the tip.

Moist shaded ground at 50–1,000 meters elevation near the coast and up to 2,100 meters in the interior; southern coastal Alaska; Vancouver Island, British Columbia; Puget Sound region; western Oregon to Humboldt County and the Sierra Nevada and San Bernardino Mountains, California; most common in the mountainous parts of the Great Basin in eastern Washington, Oregon, and California and in Idaho and western Montana; Yellowstone National Park and the Bighorn Mountains, Wyoming. On the Pacific slope the plant is localized mostly where rivers cut through the Cascade Mountains from the Great Basin. Northwestern coniferous and (mostly) yellow pine forest. May to July.

At Snoqualmie Falls, Washington on May 4, 1929, this species was found to be in flower and young fruit (*L. Benson 1228, 1229, 1230*) while *R. Bongardi* growing with it was not yet in flower (*L. Benson 1231*). Where the species and variety grow together, the characters of *R. Bongardi* and var. *tenellus* occur sometimes in various recombinations. However, the mostly coastal *R. Bongardi* and the largely interior var. *tenellus* are significantly different in several characters, and, despite intergradation, some might maintain them as separate species. The presence or absence of hair on the fruit has been adopted as an arbitrary criterion for segregating intermediate plants having characters of both the typical species and the variety.

Type collections: (1) *R. tenellus,* "Shady woods of the Oregon [Columbia] and Wahlamet [Willamette] Rivers, *Nuttall!*" (2) *R. Nelsonii glabriusculus,* "*R. nelsonii tenellus* Gray, Proc. Amer. Acad. viii, 374 (1872); *R. tenellus* Nutt.; Torr. & Gray Fl. i, 23. (1838), not Viviani. . . . Rich bottoms near Lapwai Agency, Nez Perces County, Idaho; May 5 (No. 126). Also on Clearwater River near mouth of Big Potlatch River and in the valley of the Little Potlatch." Apparently the name is merely a new one for *R. Nelsonii* var. *tenellus,* and none of the three collections listed (made by J. H. Sandberg and assistants in 1892) is intended as a type. (3) *R. Douglasii,* "*R tenellus Nutt. T. & G. Fl. i. 23. not Viviani.* . . . Common in moist places and river bottoms, California to Brit. Columbia." Since no specimen is mentioned, *R. Douglasii* is believed to have been proposed as a new name for *R. tenellus* Nutt. and to be based upon the same type. (4) *R. arcuatus.* Nomen novum for *R. tenellus* Nutt.

Significant specimens: cf. L. Benson, Am. Jour. Bot. **23**: 31. 1936.

9B. RANUNCULUS BONGARDII var. **Earlei** (Greene) L. Benson, comb. nov. *Ranunculus Earlei* Greene, Pittonia **4**: 15. 1899.

Perennial; basal leaves larger than the cauline, or only the bracts present, pilose with hairs 1–1.3 mm. long; petals obovate, 3.5–7 mm. long by 2–3 mm. broad; achenes 15–40 in a subglobose or ovoid head, each 3 mm. long, the beak 1 mm. long, 0.5–0.7 mm. broad at the base; receptacle in fruit 3 mm. long, ovoid; otherwise like var. *tenellus.*

Along streams at 2,250–2,550 meters elevation; near Mt. Hesperus and Mancos and in Delta and San Miguel Counties, Colorado. Yellow pine forest. June.

Related to *R. acriformis* A. Gray.

Type collection: "Along the Mancos River and other streams, June 22, and 28, Baker, Earle, and Tracy (38, 39, 187)." *Baker, Earle, & Tracy 38,* collected along "Mancos River Bottoms, 7,000 ft." is designated as a LECTOTYPE. It is *HGr. 2565.*

Significant specimens: COLORADO: Mancos River, *Baker, Earle, & Tracy 38,* HGr, B, US, NY; *39,* HGr, B, NY; Bob Creek, West La Plata Mountains, west of Mt. Hesperus, *Baker, Earle, & Tracy 187,* HGr, NY, GH; Leroux Creek, Delta County, *Cowen 29* in 1892, NY; Umcompahgre Plateau, West Fork of Dry Creek, *Tidestrom 1556,* US; Trout Lake, San Miguel County, *Payson & Payson 4148,* GH.

10. RANUNCULUS MACOUNII Britt. Trans. N. Y. Acad. Sci. **12**: 3. 1892. *Ranunculus hispidus* Michx. var. *oreganus* A. Gray, Proc. Am. Acad. **21**: 376. 1886. *Ranunculus oreganus* Howell, Fl. N. W. Am. **1**: 19. 1897. *Ranunculus Macounii* var. *oreganus* Davis, Minn. Bot. Studies **2**: 469. 1900. *Ranunculus rudis* Greene, Ottawa Nat. **16**: 33. 1902. *Ranunculus oreganus Macounii* Piper, Contr. U. S. Nat. Herb. **11**: 276. 1906. *Ranunculus rivularis* Rydb. Bull. Torrey Club **39**: 319. 1912.

Muddy ground of marshes, lake and stream borders, and ditches from sea level on the north coast to 2,400 meters elevation in the Rocky Mountains; Siberia; Alaska to Labrador (Lake Melville) and Newfoundland and southward to California (Goose Lake), eastern Arizona, montane New Mexico, Iowa, and Michigan (Isle Royle). Late May to August.

A geographically isolated glabrous form (var. *oreganus*) occurs at Pullman, Washington, along the lower Columbia River, and in Alaska and Siberia. In the northern part of the range of *R. Macounii* adventitious rooting is not found or is at least uncommon. Rydberg, *loc. cit.,* has proposed segregation of the rooting form as a separate species. This certainly is not justified, although it is possible that the plant might be recognized as a variety. As far as it is possible to judge from herbarium sheets, the nonrooting form occurs mostly from Washington to Colorado and northward and the rooting form occurs in those states and southward. However, adventitious roots occur on even some plants from Newfoundland. Herbarium specimens are inadequate for a clear segregation of the two forms, and other characteristics do not seem to be clearly associated with rooting and nonrooting. Much of the southwestern material is perennial, and many of the erect plants from especially the northern part of the range are apparently annual. One specimen with flowers and young fruit (Round Lake, Mackenzie Basin, northeastern Alberta, *Raup 2361,* NY.) shows the pair of cotyledons still attached to the diminutive plant in anthesis. A larger plant (*Raup 2360,* NY.) from Lake Mamawi, Mackenzie Basin is almost undoubtedly annual also, but of normal size, and a normal-sized duplicate of *Raup 2361* is in the Gray Herbarium.

The plant keyed out near *Ranunculus recurvatus* is *H. M. Raup 2367* from a slough margin at Wood Buffalo Park, Mackenzie Basin. This plant and some other specimens from the vicinity may be confused with *R. recurvatus* and *R. Bongardi*, but apparently they are reduced forms of *R. Macounii.*

Type collections: (1.) Var. *oreganus,* based upon "*R. nitidus,* in part, Hook. Fl. i. 20—Shady and wet grounds, Oregon, on the Columbia, to Fraser River." According to Hooker, *l. c.,* "Abundant on the lower fertile plains of the Columbia, where it attains a height of 1½ to 2½ feet, extending into the mountain valleys, where it is of humbler growth. *Douglas.*" (2.) *R. Macounii,* based upon *R. hispidus* Hook. Fl. Bor. Amer. **1**: 19. 1829, not Michx. in 1803. "Banks of rivers from Canada to near the mouth of the Mackenzie River lat. 67°; and from the shores of Hudson's Bay to the Pacific. *Dr. Richardson. Drummond. Scouler. Douglas.*" (3.) *R. rudis,* "Discovered in a wet meadow in Devil's Garden, northern California, (Plumas or Lassen County) June, 1895, by *Mrs. R. M. Austin.*" The type is *HGr. 2796–7.* (4.) *R. rivularis,* "NEVADA: Huntington Valley, August, 1868, *S. Watson 27* (type, in herb. Columbia University)." New York Botanical Garden.

11. RANUNCULUS PENSYLVANICUS L. f. Suppl. 272. 1781.

Wet ground of woods, meadows, and bottom lands at low or moderate elevations; China; Juneau, Alaska to Puget Sound, Yakima, and northeastern Washington and eastward across Canada and the two northernmost tiers of states to Newfoundland and New Jersey; occasional southward in the Rocky Mountains as far as northeastern Arizona and New Mexico (Rio Arriba County and the Datil Mountains).

The plants from Arizona and New Mexico have shorter fruiting receptacles and so also have specimens from Itasca Park, Minnesota (*Mayer 318, NY*).

Type collection: "*Habitat* in Pensylvania."

Significant specimens: ALASKA: Juneau, *Anderson 461,* NY. WASHINGTON: cf. L. Benson, Am. Jour. Bot. **23**: 32. 1936. MONTANA: East Gallatin swamps, *Rydberg 478,* NY; Big Fork, *B. T. Butler 7002,* NY; *7010,* NY; Columbia Falls, *R. S. Williams* in 1892, NY. IDAHO: Falks Store, Canyon County, *Macbride 316,* NY; Rathdrum, Kootenai County, *Sandberg, MacDougal, and Heller 732,* NY. ARIZONA: Ryan Ranch, East Fork of White River, *Harrison 4868,* Sac.

For the spelling of the specific name, cf. Fern. Rhodora **42**: 94–5. 1940.

12. RANUNCULUS MACRANTHUS Scheele, Linnaea **21**: 585. 1848. *Ranunculus repens* L. var. *macranthus* A. Gray, Bost. Jour. Nat. Hist. **6**: 141. 1845.

Moist meadows at about 2,000 meters elevation in Eastern Arizona from Navajo County to the Santa Rita and Huachuca Mountains and at lower elevations in Western and Southern Texas; Mexico. Yellow pine and southern hardwoods forests; Gulf grassland. June and July in Arizona and March and April in Texas.

Type collection: "Prope Neubraunfels leg. Römer. Aprili." Texas.

13. RANUNCULUS ORTHORHYNCHUS Hook. Fl. Bor. Amer. **1**: 21. *pl. 9.* 1829. *Ranunculus ornithorhynchus* Walp. Rep. **1**: 43. 1842, error in spelling. *Ranunculus orthorhynchus* "form" *stenophyllus* A. Gray, Proc. Am. Acad. **21**: 377. 1886.

Stems 1.5–5 dm. long and 1.5–3 or 4 mm. in diameter, fistulous, hirsute, the hairs ascending and tending to be appressed; radical leaf blades pinnate with 3–7 leaflets, the leaflets alternate or opposite, again twice-forked or -lobed, the divisions all (typically) linear or else cuneate, ultimate lobes acute, appressed-pubescent or nearly glabrous; petioles 3–12 cm. long; sepals 5, greenish-yellow, pilose dorsally; petals yellow or (in the Northwest) often red dorsally, 8- or 10–19 mm. long, 4–7 mm. broad; achenes 12–20, each achene elliptic, 3 mm. long, 2.3 mm. dorsoventrally, 0.5 mm. laterally, margin prominently bevelled and slightly keeled, the achene beak slender, about 4 mm. long, straight; receptacle nearly cylindrical, 1–2 mm. long in flower and 2–3 mm. long in fruit, hispidulous.

Meadowland at low elevations along the northwest coast and at 1,500–2,000 meters elevation southward; Pacific slope from Vancouver Island to western Oregon; Goose Lake, middle north Coast Ranges, and central Sierra Nevada, California; one fragment from Yellowstone National Park. Northwestern coniferous and yellow pine forests. May and June.

Where *Ranunculus orthorhynchus* crosses the range of var. *platyphyllus* in southwestern Oregon and adjacent California, intergrades are abundant. The Sierra Nevada plants are also intermediates, and their assignment to *R. orthorhynchus* is rather arbitrary.

Type collections: (1) *R. orthorhynchus*, "Not unfrequent on the low points of land near rivers, in North-West America. *Douglas.*" (2) "Form" *stenophyllus*, "The typical form of *R. orthorhynchus*, STENOPHYLLUS, has all the leaves somewhat bipinnately dissected into segments a line or less in width, or some radical ones simply divided into cuneate or obovate 2–3-lobed or toothed segments or leaflets." The type must be identical with that of *R. orthorhynchus.* Gray cited no specimens or localities for the "form."

13A. RANUNCULUS ORTHORHYNCHUS var. PLATYPHYLLUS A. Gray, Proc. Am. Acad. **21**: 377. 1886. *Ranunculus maximus* Greene, Bull. Torrey Club **14**: 118. 1887. *Ranunculus orthorhynchus* var. *maximus* Jepson. Fl. W. Mid. Calif. 200. 1901. *Ranunculus politus* Greene, Pittonia **5**: 196. 1903. *Ranunculus platyphyllus* A. Nels. Bot. Gaz. **42**: 52. 1906. *Ranunculus platyphyllus* Piper, Contr. U. S. Nat. Herb. **11**: 276. 1906.

Stems 6–12 dm. long, often 7–9 mm. in diameter, hirsute, sometimes rather densely so; basal leaves pinnate with 5–7 leaflets; sepals hirsute dorsally; petals broader and shorter than in the typical species, rarely red dorsally (southern Oregon); achenes 20–35, achene beak 2.5–3.5 mm. long and less rigid than in the typical species, sometimes very nearly hooked at the apex; receptacle elongated from 2–3 mm. long in anthesis to 5–9 mm. long (and expanded to 2–3 mm. in diameter) in fruit.

Meadows from sea level on the coast to 2,200 meters elevation in the interior; California along the coast from Del Norte County to Berkeley;

upper Sacramento Valley and at Stockton; mountains of the Great Basin from the southern edge of British Columbia to eastern Oregon, Nevada (Gold Creek), Utah (Wasatch and Uintah Mountains), Wyoming (West De Lacy Creek and Teton Pass), and Glacier National Park, Montana (San Marias Pass, *Somes 90*). Northwestern coniferous and western pine forests and Pacific grassland. June and July.

Apparently originally introduced into California by the Klamath River, which intersects the range of *Ranunculus orthorhynchus*. Where the ranges of the species and variety overlap, hybridization is frequent, and segregation is difficult.

Type collections: (1) Var. *platyphyllus*, "*R. macranthus*, Watson, Bot. King Exped. and Bot. Calif., not Scheele.—In wet places, Wahsatch Mountains and Idaho to E. Oregon, and California, south to Marin Co." The following is quoted from Watson, Rept. U. S. Geol. Expl. 40th Par. **5**: 9. 1871, "RANUNCULUS MACRANTHUS, Scheele. . . . Texas, California, (4,729 Bolander), and Oregon, (Lyall.) Streambanks in the Wahsatch and Uintas; 5–8,000 feet altitude; June, July. (28)." The specimen in the Gray Herbarium from the Wasatch Mountains, *S. Watson 28*, collected in 1869, is designated as a lectotype. (2) *R. maximus*. "*R. macranthus*, Brew. & Wats., Bot. Cal. i. 8, not of Scheele; *R. orthorhynchus*, var. *platyphyllus*, Gray, Proc. Am. Acad. xxi. 377, as to the Californian plant at least." Brewer and Watson refer the reader to "Watson, Bot. King 9," and they state further, "Moist soils from Oregon to Nevada and Texas. In this state [California] near the coast." The reference to *R. orthorhynchus* var. *platyphyllus* includes specifically only the "Californian plant." Since both var. *platyphyllus* and *R. macranthus* of the Botany of California were based upon Watson's previous publication (Rept. U. S. Geol. Expl. 40th. Par. 5: 9. 1871, as cited above), the single California specimen mentioned there is designated as a lectotype. It is *Bolander 4729* from Long Valley Mendocino County. LECTOTYPE in the Gray Herbarium.

13B. RANUNCULUS ORTHORHYNCHUS var. HALLII Jepson, Fl. Calif. **1**: 542. 1922.

Hair of stems and petioles spreading; leaf divisions often as broad as long, shallowly and obtusely lobed; achenes 4–17, usually few, the marginal keel of each more distinctly carried into the beak than in the typical species; otherwise like the typical species.

Mountain meadows at about 2,000 meters elevation; Sierra Nevada from Yosemite National Park to Fresno County, California. Yellow pine forest. June and July.

Type collection: "Pine Ridge, Fresno Co., Hall and Chandler 236 (type)."

Significant specimens: cf. L. Benson, Am. Jour. Bot. **23**: 31–32. 1936.

13C. RANUNCULUS ORTHORHYNCHUS var. **alaschensis** L. Benson var. nov.

Stems 6–7 dm. long, 2–4 mm. in diameter, markedly fistulous, glabrous; basal leaves with 3 or 5 leaflets, the terminal leaflet 3-lobed and the lobes again notched, the lateral leaflets opposite or nearly so, cuneate to obdeltoid, 15–30 mm. long, of 13–30 mm. maximum breadth, the ultimate lobes rounded and the sinuses acute, petioles 15–20 cm. long; cauline leaves more dissected than in the typical species and with acute ultimate lobes; sepals glabrous, tinged with purple; petals 5, yellow on both sides, obovate, 11–12 mm. long, 6 mm. broad; achenes 10–20, the achene body 4 mm. long, 3 mm. broad, the margins not markedly beveled or keeled, the beak straight or a little curved at the tip, 3 mm. long; receptacle but slightly enlarged in fruit, hirsute.

Herba terrestris perennis glabra; caulibus 6–7 dm. longis, 2–4 mm. diametro, glabris; foliis 3–5-foliolatis, foliolis cuneatis vel obdeltoideis, tridentatis, 30 mm. longis, 13–30 mm. latis; petiolis 15–20 cm. longis; sepalis glabris; petalis 5, luteis, obovatis, 11–12 mm. longis, 6 mm. latis; acheniis 10–20, obovatis, 4 mm. longis, 3 mm. latis; rostro filiformi, 3 mm. longo.

Moist ground at low elevations; Yes Bay and Anan Creek, south coast of Alaska. Northwestern coniferous forest. July.

Type collection: Shores of Yes Bay, Alaska, July 20, 1895, *Thos. Howell, Howell's Pacific Coast Plants No. 1603.* TYPE in the New York Botanical Garden.

Significant specimens: ALASKA: Yes Bay, *Howell 1603,* NY, HGr; *Gorman 61,* NY; Anan Creek, mainland, *Walker 761,* NY, GH.

14. RANUNCULUS BLOOMERI S. Wats. Bot. Calif. **2**: 426. 1880.

Very wet and heavy soil of meadows, sloughs, and ditches; Mendocino and Lake Counties to Santa Clara County, California. Oak woodland. March to early May.

Intergrades with *Ranunculus orthorhynchus* var. *platyphyllus* occur abundantly in western Lake County and northeastern Sonoma County.

Type collection: "In wet grounds near San Francisco, *Dr. J. G. Bloomer.* The specimens are imperfect and not yet in fruit, but indicate a very distinct species."

15. RANUNCULUS CAROLINIANUS DC. Syst. **1**: 292. 1818.

Swampy ground at low elevations near the coast; Alabama to North Carolina and Florida. River bottom forest. March to May.

Type collection: "Hab. in Carolina inferiore. *Bosc.*"

This species has been known as *R. palmatus* Ell.; cf. Fern. Rhodora **41**: 543–4. 1939.

Table 2 contrasts *Ranunculus carolinianus* with its eastern relatives, *R. hispidus* and *R. septentrionalis:*

16. RANUNCULUS SEPTENTRIONALIS Poir. in Lam. Encyc. Meth. **6**: 125. 1804. *Ranunculus lucidus* Poir. in Lam. Encyc. Meth. **6**: 113. 1804 (?). *Ranunculus tomentosus* Poir. in Lam. Encyc. Meth. **6**: 127. 1804, not Moench in 1794. *Ranunculus Belvisii* DC. Syst. **1**: 291. 1818. *Ranunculus nitidus* Muhl. Cat. Ed. 2. 56. 1818, not Walt. in 1788. *Ranunculus intermedius* Eat. Man. Bot. Ed. 3. 424. 1822, not Poir. in 1804. *Ranunculus Schlectendalii*

TABLE 2

	R. carolinianus	*R. hispidus*	*R. septentrionalis*
Petal breadth	2–3 or rarely 4 mm.	4–7 or rarely 3 or 11 cm.	4–8 or 13 cm.
Sepal habit	Reflexed	Spreading	Usually spreading
Comparative length of sepals to petals	Half	Half	Two-thirds to three-fourths
Achene number	7–15	12–30	15–30
Stoloniferous	Rarely	Never	Frequently (if not always) after flowering
Stem diameter	0.7–1.5 or 2 cm.	1.5–2.5 cm.	1.5 or 2–8 cm.
Stamen number (approximation)	20–40	40–60	40–75
Length of fruiting receptacle	2–3 mm.	4–8 mm.	4–8.5 mm.

Hook. Fl. Bor. Amer. **1**: 21. 1829. *Ranunculus septentrionalis* var. *nitidus* Chapm. Fl. S. U. S. Ed. 2, Suppl. 675. 1892. *Ranunculus octopetalus* Greene, Ottawa Nat. **16**: 33. 1902. *Ranunculus caricetorum* Greene, Pittonia **5**: 194. 1903. *Ranunculus sicaeformis* Mack & Bush apud Mack., Torreya **6**: 123. 1906. *Ranunculus sicaefolius* Mack. & Bush ex Rydb. Fl. Prairies & Plains of Central No. Amer. 342. 1932, *nomen nudum*, apparently intended for *R. sicaeformis*. *Ranunculus septentrionalis* var. *caricetorum* Fern. Rhodora **38**: 177. 1936.

Subglabrous to densely hispid; stems erect and 2–6 dm. high or (in summer) at least sometimes stoloniferous; radical leaf blades compound or occasionally simple and 3-lobed, broadly ovate-cordate in outline, 3–14 cm. long, 5–20 cm. broad, the leaflets 3-lobed, -cleft, or -parted and again toothed or lobed, the blade proximally truncate or cordate and distally angular, subglabrous to appressed-hispidulose; sepals spreading or (in some Middle-Western plants) reflexed; achenes about 15–30, each achene obovate, 3–3.5 mm. long, 2–2.5 mm. dorso-ventrally, 0.7 mm. laterally, the achene beak stout at the base, slender above, 2–3 mm. long, straight; receptacle 4–8.5 mm. long in fruit.

Marshy ground at mostly low elevations; Eastern South Dakota and Nebraska to James Bay and to Battle Harbor, Labrador and southward to Missouri, Kentucky (*Short* in 1840, N.Y.), West Virginia, and the Virginia Coastal Plain; Fulton, Arkansas and Austin, Texas. April to early June (July or August northward).

Reported by Fernald (Rhodora **22**: 31. 1920) to produce long stolons very soon after the beginning of flowering. The writer has collected this species only once (in Pennsylvania in June, 1935), and in this case field observation revealed an abundance of stolons. Most herbarium specimens do not show stolons. The densely retrorsely-hispid form occurring here and there in the Middle West and at Cumberland, Maryland (*Shriver* in 1894, NY) is var. *caricetorum* (Greene) Fern.

Type collections: (1) *R. septentrionalis,* "Cette plante croît dans l'Amerique septentrionale . . . in herb. Lamarck." (2) *R. lucidus,* "Cette plante est cultivée au Jardin des Plantes de Paris. On soupçonne originaire du Levant." (3) *R. tomentosus,* "Cette plante a été recueillie par M. Bosc dans la Haute-Caroline." (4) *R. Belvisii,* "Hab. in America boreali. *Pal. de Beauvois.*" (5) *R. nitidus,* "Car." Carolina. Type in the herbarium of Muhlenberg. (6) *R. intermedius,* "Found on the banks of the Hudson near Albany, by Mr. J. G. Tracy." (7) *R. Schlectendalii,* "R. fascicularis, *Schlect. Animadv.* Sect, 2, p. 30. t. 2. . . . Eastern declivity of the Rocky Mountains, between lat. 52° and 55°, in rich soils: plentiful. *Drummond.*—This plant agrees in every particular, as far as I can judge without fruit, with the description and figure above quoted of Schlectendal's *R. fascicularis,* except that his figure represents a slenderer plant, and one of the leaves has the middle lobe petioled, and the calyx reflexed. . . ." Asa Gray, Proc. Am. Acad. **21**: 372–3, 376. 1886, designated Schlectendal's specimen as a LECTOTYPE for *R. Schlectendalii.* (8) *R. octopetalus,* "Knox Co., Tennessee, 10 June, 1893, T. H. Kearney." The TYPE specimen is *HGr. 2739,* and the specimen from marshes near Fountain City, *Kearney,* June 10, 1893, *HGr. 2738,* is probably part of the same collection. (9) *R. caricetorum,* "The above diagnosis is from material of my own gathering in southern Wisconsin in 1888, and in southern Michigan in 1902." The specimen from Dodgeville, Wisconsin, collected by Greene June 20, 1898, is designated as a lectotype. It is *HGr. 2559–60–61.* (10) *R. sicaeformis,* "Collected by myself (no. 95) at Buckner, Jackson County, Missouri, on May 30, 1898 . . . in my herbarium," *K. K. Mackenzie.* The TYPE is now in the New York Botanical Garden.

Table 3 contrasts *Ranunculus septentrionalis* with its Pacific Coast and Rocky Mountain relatives:

TABLE 3

	R. septentrionalis	*R. orthorhynchus*	*R. Bloomeri*
Stem habit	Stoloniferous or often so	Never rooting	Never rooting
Radical leaf leaflet No.	1–3	3–7	3–5
Sepal habit	Spreading or rarely reflexed	Reflexed	Reflexed
Comparative length of sepals to petals	Two-thirds or three-quarters	One-third or one-half	One-half or two-thirds
Pubescence	Usually subglabrous but occasionally hispid	Hispid	Subglabrous

16A. RANUNCULUS SEPTENTRIONALIS var. **pterocarpus** L. Benson, var. nov.

Subglabrous; more markedly stoloniferous than the typical species; radical leaves simple or of 3 leaflets, these more shallowly lobed and toothed than in the typical species, crenate or serrate; sepals reflexed or spreading; achenes 5–15, the bodies obovate to suborbicular, 3.5–4.3 mm. long, 3.3–4 mm. broad, including the winged keels, which may be up to 1 mm. broad, the achene beaks about 2 mm. long; fruiting receptacle 4–5 mm. long.

Herba palustris perennis subglabra; stolonifera; dentibus foliorum brevibus; acheniis 5–15, obovatis vel suborbicularibus, 3.5–4.5 mm. longis, 3.3–4 mm. latis, alatis; receptacula 4–5 mm. longo.

Marshy ground at low elevations; Wyandotte County, Kansas to Illinois, Indiana, Kentucky, and Tennessee; occurring as an intergrade to *R. palmatus* in southern Alabama and Florida; Dallas County, Texas. Southern deciduous and river bottom forests. May and June.

Type collection: Wet soil, Red River bottom near Boss, McCurtain County, Oklahoma, *H. W. Houghton 3732½*, May 23, 1916. TYPE in the New York Botanical Garden. An isotype is in the Gray herbarium.

Representative specimens: KANSAS: Wyandotte County, *Hitchcock 1105,* NY, GH. MISSOURI: St. Louis, *Riehl 25* in 1838, NY, *Eggert* in 1877, GH; Campbell, Dunklin County, *Palmer 39066,* GH. ILLINOIS: Mound City, HGr *16775*; Macon County, *Clokey 2384,* GH; Starved Rock, La Salle County, *Greenman, Lansing, & Dixon 123,* NY, GH. INDIANA: *Torr. & Gray, Fl. N. Amer.,* GH. KENTUCKY: Near State Lake, *Shacklette 273,* NY. TENNESSEE: Humboldt, Tennessei occidentalis, *Bain 383,* NY. OKLAHOMA: Boss, McCurtain County, Red River bottom, *Houghton 3732½,* NY, GH. TEXAS: Dallas County, *Reverchon 2739,* NY; Dallas, *Reverchon* in 1874, GH; San Felipe, *Lindheimer* in 1844, GH; Brazos River, *Drummond* in 1835, GH; Columbia, *Bush 147* GH; Blooming Grove, *Reverchon 3700,* GH. ALABAMA: Catoma Creek, Montgomery County, *Harper 85,* NY, GH. FLORIDA: Ocklocknee River, Leon County, West of Tallahassee, *Small & Wherry 11670,* GH, NY.

17. RANUNCULUS HISPIDUS Michx. Fl. Bor. Amer. **1**: 321. 1803. *Ranunculus marilandicus* Poir. in Lam. Encyc. Meth. **6**: 126. 1804 (?). *Ranunculus palmatus* Ell. Sketch. **2**: 61. 1816. *Ranunculus repens* L. var. *hispidus* Chapm. Fl. S. U. S. Ed. 1. 8. 1860. *Ranunculus septentrionalis* Poir. var. *marilandicus* Chapm. Fl. S. U. S. Ed. 3. 8. 1897 (?). *Ranunculus hirtipes* Greene, Ottawa Nat. **16**: 32. 1902.

Hirsute terrestrial perennials; roots usually fleshy, commonly 1.5–2.5 mm. in diameter; stems 1.5–3 mm. in diameter, fistulose, hirsute, the hairs sometimes appressed especially in specimens from Ontario, New York, and eastern Pennsylvania; radical leaf blades nearly always pinnately compound, cordate-ovate in outline, laciniate, 4–9 cm. long, 5–11 cm. broad, the terminal leaflet 3- and the lateral leaflets 2-parted, the parts sharply lobed or serrate-laciniate-toothed, blades proximally subcordate and distally acute, appressed-hirsute, the hairs rarely abundant; each achene obovate, 2.3–2.9 mm. long, 1.8–2.3 mm. dorso-ventrally, 0.7 mm. laterally, the achene beak slender, 1–2 mm. long, straight.

Moist places in meadows and rich woods at low elevations; Valley City, North Dakota, and Newark, Nebraska, to Ontario, Massachusetts, Missouri, Arkansas (modified form), Tennessee, and New Jersey; less common southward along the Atlantic Coast to Hendersonville, North Carolina and Atlanta, Georgia. Mostly Southern deciduous forest. April and May.

A form with radical leaves 8–10 cm. long and 12–16 mm. broad occurs in McDowell and Randolph Counties, West Virginia (Spruce Mountain

Branch of the Condon Lane Boom and Lumber Company Railroad, *Moore 2225*, GH; Railroad track, Allegheny Mountains, Randolph Co., *Greenman 366*, GH; Welch, *Webb* in 1922, GH). The leaf size and type are approached by plants from other parts of the west side of the Appalachian system. The leaf divisions are from narrowly elliptic to obovate. Segregation of varieties in *R. hispidus*, which is a polymorphic species, is difficult. The two listed below are well-distinguished in their extreme forms, but countless intermediate forms occur. From herbarium sheets distinction of *R. hispidus* from *R. septentrionalis* is not (apparently) always possible.

Type collections: (1) *R. hispidus*, "HAB. in umbrosis sylvis Carolinae inferioris." (2) *R. marilandicus*, "Cette plante croîte au Maryland . . . in herb. Bosc." This plant may be var. *falsus*. (3) *R. palmatus*, "Grows in St. John's Berkley." Near Savannah, Georgia. (4) *R. hirtipes*, "Obtained in woods near Sandwich, Ontario, 5 June, 1901, by Mr. John Macoun . . . bearing the Canad. Geol. Survey number 33,582." The TYPE is HGr. 2619.

17A. RANUNCULUS HISPIDUS var. FALSUS Fern. Rhodora **22**: 30. 1920.
Ranunculus cardiopetalus Greene, Ottawa Nat. **16**: 32. 1902.

Stems 1–2 mm. in diameter, almost always appressed-pubescent, the hairs softer than in the typical species; the stems less markedly fistulose than in the typical species; radical leaf blades either simple and 3-parted or, if compound, the leaflets usually sessile and close to one another, less dissected than in the typical species, usually 1.5–4 mm. long, 2–5 mm. broad, but occasionally larger; fruit smaller than in the typical species and with a narrower keel (as pointed out to the writer by M. L. Fernald).

Dry or rocky woodland at low elevations; occasional from Toledo, Ohio to Pickett County, Tennessee; Ontario (Niagara Falls) to southwestern Vermont, Massachusetts, and Washington, D. C.; rare and modified in Virginia, North Carolina, and Alabama. Northeastern and Southern deciduous forests. April and May.

This variety is marked by small and most commonly simple leaves and by appressed pubescence and small fruit. Other forms are looked upon as intermediates, that is, if they show one of the characters and not the other.

Type collections: (1) *R. cardiopetalus*, "At the whirlpool Rapids, Niagara, Ont., 21 May, 1901, John Macoun (n. 33,581)." The TYPE is *HGr. 2546*. It has emarginate petals. (2) Var. *falsus*, "Dry wooded calcareous bank, Sheffield, May 30, 1919, Bean & Fernald. (TYPE in Gray Herb.)"

17B. RANUNCULUS HISPIDUS var. **eurylobus** L. Benson, var. nov.

Stems 1.2–2 mm. in diameter, very densely hirsute, the spreading hairs 2 mm. long; radical leaf blades mostly simple, the leaflets when present sessile and usually close to one another, the simple leaves lobed or divided, the leaflets or lobes or the whole leaf tending to be very broad or even orbicular, rounded at the bases, the leaf or leaflet 2–5 cm. long, 2–5 cm. broad.

Caulibus valde hirsutis; foliis vel foliolis latissimi vel orbicularibus, a basibus rotundis, 2–5 cm. longis, 2–5 cm. latis.

Hill country toward the interior from West Virginia and from Arlington, Brunswick County, and Fort Myer, Virginia, to Georgia and Alabama; Monterey, Tennessee; occurring in modified form in Kentucky and Tennessee and along the southern Atlantic coastal plain. March and April.

Type collection: "Oak woods, dry, Augusta, Georgia, March 26, 1899." TYPE in the New York Botanical Garden. Unfortunately the collector's name is not on the specimen, which is labelled in pencil. Although the variety has been collected rather frequently, no other specimen is suitable for a type.

Significant specimens: TENNESSEE: Monterey, *Cain & Sharp 4352,* NY. ALABAMA: Warrior River, Tuscaloosa, *Harper 3014,* NY. WEST VIRGINIA: Milton, Cabel County, *L. Williams 411,* NY. VIRGINIA: Arlington, *Blanchard* in 1891, NY; Meherrin River, 8 miles southeast of Cohran, Brunswick County, *Fernald & Long 7027,* GH; Fort Myer, *Mearns* in 1895, NY. NORTH CAROLINA: Tryon Mountain, Polk County, *Huger* in 1896, NY; Roanoke River at Weldon, *Small* in 1897, NY. SOUTH CAROLINA: Clemson College, Oconee County, *House 1712,* NY; Andersonville, *Earle* in 1886, NY. GEORGIA: Large Knob, Kenesaw Mountain, *Perry & Myers* in 1934, NY; Thompson Mills, Gwinnett County, *Allard 47* in 1908, NY.

18. RANUNCULUS FASCICULARIS Muhl. ex Bigel, Fl. Bost. Ed. 1. 137. 1814. *Ranunculus fascicularis* var. *Deforestii* Davis, Minn. Bot. Studies, **2**: 470. 1900. *Ranunculus illinoensis* Greene, Pittonia 5: 195. 1903.

Stems 1–2 dm. long; radical leaf blades compound or the early ones 3-parted, ovate-oblong in outline, 2.5–5.5 cm. long, 2–4 cm. broad, distinctly longer than broad, leaflets 3 or commonly 5, sometimes the leaf partly bipinnate, the leaflets deeply 3–7-parted and again angularly-toothed, the ultimate parts blunt at the apices; petals 5 or rarely 9 (1 specimen), 7–15 mm. long; each achene obovate-orbicular with a short, flat stalk, the main body 1.5–2.5 mm. long, 1.5–2 mm. dorsoventrally, 0.6–1 mm. laterally, the margin keeled but not prominent.

Rather dry situations at low elevations; Taylor Falls, Minnesota, to southern Ontario, New England (except Maine and Rhode Island), New Jersey, and Pennsylvania (Lancaster) and southward to Oklahoma and Tennessee; "Southern Flora" (*Chapman,* NY; sepals reflexed). Northeastern and Southern deciduous forests. March to May, depending upon latitude; commonly called "early buttercup."

Truly tuberous roots are rare in specimens from east of the Mississippi Valley.

Type collections: (1) *R. fascicularis,* "The plants described in this book have been collected during the two last years in the vicinity of Boston, within a circuit of from 5 to 10 miles." 1812–13. (2) Var. *Deforestii,* "Collected by Henry P. DeForest (G. 42) near Rossville, Ill., April 12, 1885." The type specimen in the herbarium of Cornell University was kindly loaned to the writer by Dr. K. M. Wiegand. Some of the flowers have 9 petals and some have 5. (3) *R. illinoensis,* "Collected at Alto Pass, in southern Illinois, 21 April, 1900, by Mr. Carl F. Baker, who reports that it occurs in large patches on moist open hillsides.'' Possibly a variety, but the type must be reexamined for characters other than the merely lobed early radical leaves, before a segregation can be made, if it is desirable. TYPE: *HGr. 2630.*

18A. RANUNCULUS FASCICULARIS var. APRICUS (Greene) Fern. Rhodora **38**: 178. 1936. *Ranunculus apricus* Greene, Pittonia **4**: 145. 1900.

Stems 1–3 dm. long; leaflets or leaf segments oblanceolate to narrowly elliptic, shallowly few-toothed apically or entire; petals 5, like those in the typical species; achenes like those of the typical species.

Mostly in the prairie country from Cherokee County, Kansas, to eastern Texas, Louisiana, and North Carollton, Mississippi; ''S. W. Colorado'' (*Flint*, NY). Prairie grassland; deciduous and river bottom forests. March and April.

The form occurring in wet ground in Louisiana and at Galveston, Texas is 2–3 dm. tall and is with usually small fruit and with less hair on the plant.

Type collection: ''Near Sapulpa, Indian Territory Oklahoma, 29 April, 1895, B. F. Bush.'' The TYPE is *Bush 965, HGr. 2493.*

18B. RANUNCULUS FASCICULARIS var. **cuneiformis** (Small) L. Benson, comb. nov. *Ranunculus cuneiformis* Small, Bull. Torrey Club **27**: 276. 1900.

Stems 18–25 cm. long; leaves like the typical species, but a little larger and coarser; petals 7–9, 13–15 mm. long when fully expanded; achene 3 mm. long by 2.5 mm. dorsoventrally, the margin 0.5 mm. broad, distinctly marked.

Moist ground; collected at Bear Creek, Kerr County, Texas, and at Natchitoches, Louisiana (Palmer 6988). Southern deciduous forest. Early spring.

Type collection: ''On prairies, near Kerrville, Texas. Spring. Heller, Pl. S. Tex. no. 1688.''

DEPARTMENT OF BOTANY, UNIVERSITY OF ARIZONA
TUCSON, ARIZONA

NOTES ON POLYGONUM (AVICULARIA)

J. F. BRENCKLE

(WITH THREE FIGURES)

PHOTOPERIODISM AND TAXONOMY

Field observations in South Dakota show that the genus *Polygonum* is strongly affected by long days of bright sunlight. Profound changes take place in the plants during late June and in July, our longest and brightest days. The large spring stem-leaves fall from the plants and fruit production is slowed or stopped entirely. While each species reacts somewhat differently, the phenomenon takes place in all forms, both early and late. The small wiry species such as *P. achoreum* and *P. buxiforme* set fruit very early, often in the axils of the second and third stem-leaf, and fruit production continues until the latter part of June when the stem leaves and fruit fall away. Some of these plants do not survive this change, but others more favorably located continue growth with shortened internodes, smaller leaves, and a more compact inflorescence. *Polygonum* species with a late habit of growth, such as the group *P. ramosissimum* which seldom blooms in June with us, also lose the basal leaves but continue growth with narrower and smaller leaves through July; blooming is delayed to late August and September. Protection from intense or prolonged periods of sunlight by cloudiness or shade may prevent this retardation of bloom. Polygonums in general from high elevations show no such retardation. A series of specimens of *P. ramosissimum* collected on July 31 and August 1, 1939, along a road from Forsythe, Montana, to Mellette, South Dakota, show a marked difference in development. The western plants are more advanced, although collected from a higher elevation and latitude than those from the eastern half of South Dakota. Specimens from a creek-bed with perpendicular walls from 10 to 15 feet high, near Miles City, Montana, had well ripened achenes. These plants were the best developed of the series, no doubt owing to the protecting shade of the sidewalls. The winding arroyo with its walls afforded shade from east, west, or south, up to 30 to 40 per cent of the day's sunlight. Six specimens of the series are herewith deposited in the herbarium of the New York Botanical Garden.

Specimens of *Polygonum* collected in midsummer during the "rest period" are often sterile or otherwise in poor condition to classify. The marked difference between the spring, summer, and fall forms is confusing unless a series of specimens is at hand to represent these stages. Abundant and well developed material of *P. rubescens* Small sent me from Alberta, Canada, by Dr. Geo. H. Turner, illustrates this. The spring leaves have a shape and size quite distinctive, are broadly elliptic or obovate, abruptly pointed at the apex, somewhat narrowed toward the base, subsessile or with a short petiole, 2–6 cm. long, 1–2.5 cm. wide. These merge into the narrow lanceolate leaves of summer and are lacking in fruiting specimens. Specimens in triplicate representing spring, summer, and fruiting stages of this plant will be deposited in the Gray Herbarium, the National Herbarium and the herbarium of the New York Botanical Garden.

THREE ALIEN POLYGONUMS IN THE WEST

POLYGONUM ARGYROCOLEON Steudel. "Silver-sheath knotweed."[1] "Erect, annual, with slender branches; leaves linear-lanceolate, often deciduous; flowerspikes slender, naked; flowers pedicelled, shortly exserted from the ocreolae; perianth about 2 mm. long; achenes equal to the perianth, brown, smooth, and shining."[2] The plant has a dark grey-green color, strikingly different from that of American species. The silvery ocreae are membranous, showy, and white. Introduced into southern California and Arizona with alfalfa seed from Persia and widespread in alfalfa and grain fields.[1]

Specimens examined: California, Santa Catalina Island, *Fosberg 4461* (as *P. ramosissimum*): Imperial County, alfalfa fields; *Bellue*, July 6, 1932.

POLYGONUM HUMIFUSUM Pall. ex Ledeb. (not *P. humifusum* Jord.). "A smooth, branching, prostrate herb; leaves linear to oblong, obtuse; inflorescence at tips of the branches, fascicles 4–10 flowered; achenes smooth, exceeding the perianth."[2] A skeleton-like plant with spathulate-linear leaves mostly divergent or reflexed; flowering from the base in the axils of all leaves; achenes lenticular or three-angled, ovate, pointed, black, smooth, and shining, about 1 mm. long (fig. 1). Three sheets of this species have been examined, all collected near Nanaimo, Vancouver Island, B.C., by *Dr. John Macoun,* and distributed under *No. 1483* (as *P. aviculare*). The sheet in the Canadian National Herbarium, Ottawa, was collected July 11, 1887, "on ballast." This plant, about 5 to 6 dm. long, has all its achenes 3-angled. A sheet in the herbarium of the University of Minnesota, Minneapolis, has three plants of about half the length of the above, collected on July 12, 1893, six years later. These have all achenes lenticular, pointed, black, smooth, and shining, about 1 mm. long. The third sheet, in the herbarium of the New York Botanical Garden, dated July 12, 1893, Nanaimo, B. C., has two plants similar in size to the Minnesota specimens, one of which has its achenes 3-angled and the other lenticular. These remarkable plants appear to belong to the section *Avicularia.* No known American species of this section has lenticular achenes. Among the *Persicariae* some species may have occasional 3-angled achenes, but the plants here represented have them either lenticular or 3-angled, with no mixture on a single plant.

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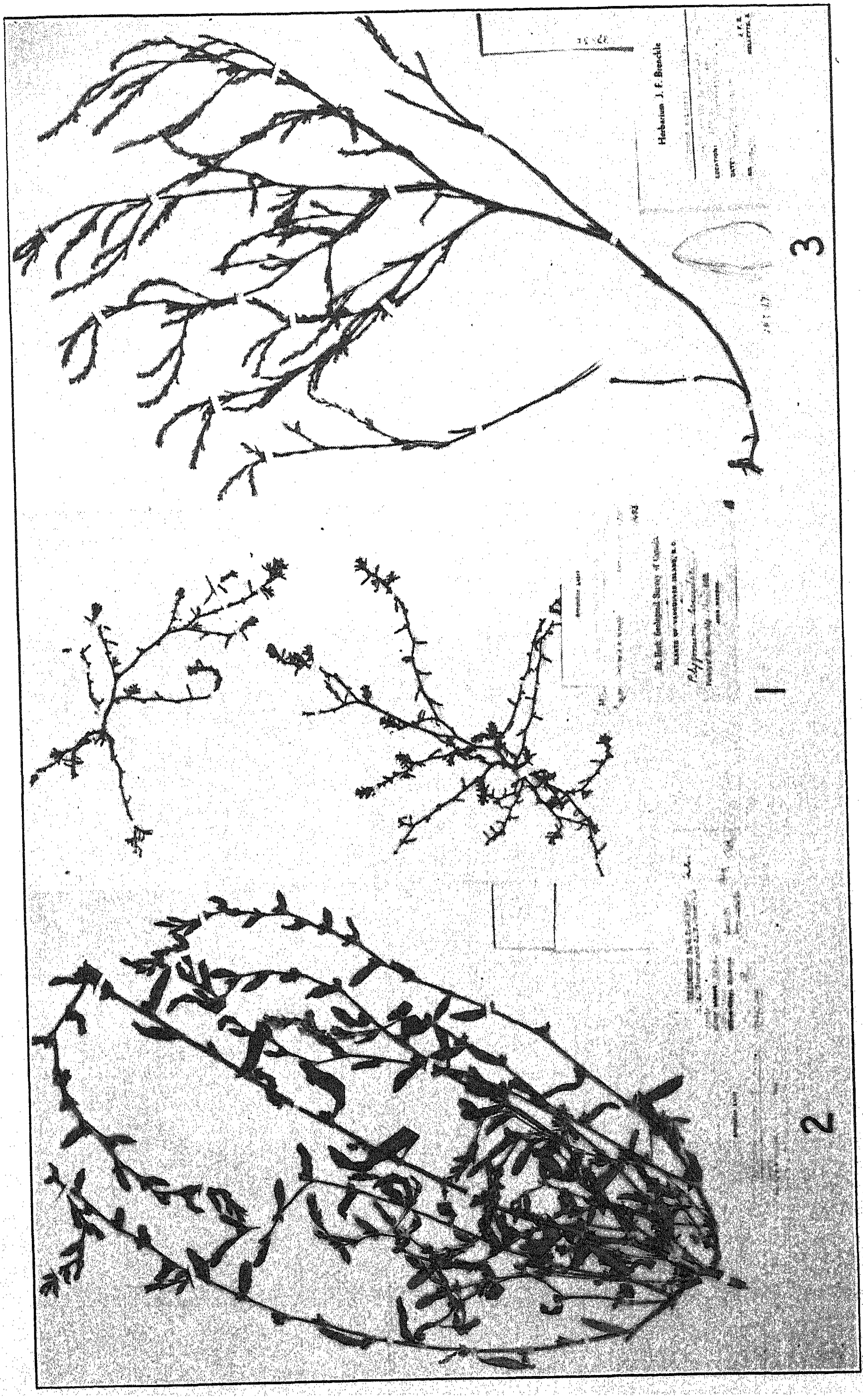
[1] Bellue, Margaret K. 1935, Silver-sheathed Knotweed as a pest in S.W. Alfalfa. Mo. Bull. Dept. Agr. Calif. June 1935: 238–241.

[2] Steward, Albert N. The *Polygoneae* of eastern Asia. Contr. Gray Herb. 87: 19. 1930.

Explanation of figures 1–3

FIG. 1. *Polygonum humifusum.* FIG. 2. *Polygonum Stevensii.* FIG. 3. *Polygonum autumnale.*


Herbarium J. F. Brenckle
3
1
2

POLYGONUM POLYCNEMOIDES Jaub. et Spach. "A prostrate branching herb with appressed linear-subulate leaves: ocreae hyaline, white, conspicuous, sometimes lacerate: flowers axillary, near the tips of the branches, sessile, about 2 mm. long: achenes triangular, black, included in the perianth; faces minutely punctate. South-central Asia."[3]

The specimens kindly sent me by Prof. Ray J. Davis, from Idaho, collected on an abandoned field, no doubt belong to this Asiatic species and were introduced with garden or field seed. The striking character which differentiates them from American species is the perianth. Grey-green, scurfy, constricted above, closely investing the mature achene; shallowly 5-parted to about one-fourth its length; the limb is spreading, white, .4–.5 mm. long. Sometimes a short white-hyaline, denticulate, ocreolus persists about the base of the perianth. The dry stems are fragile and the leaves veinless and glandular-punctate. The rather short limb probably places these plants with *P. Oliveri* Jaub. et Spach.[3]

No. 2833, Ray J. Davis, Idaho, is deposited in the New York Botanical Garden.

TWO NEW SPECIES

Polygonum Stevensii Brenckle, sp. nov. Planta annua; caulis acute angulatus, erectus, 4–7 dm. altus, base ramosus; folia crassa, oblonga, brevipetiolata, inconspicue nervata, 2–5 cm. longa, 4–10 mm. lata, tam longa vel longiora quam internodi. Ocreae inconspicuae, macrae; flores copiosi; perianthi axillares, 2–8 ad quodquam folium, pedicellati, 4–5 mm. alti. cum sex segmentis; segmenta tres exteriora carinata, nervata, cucullata, viridia, albomarginata; achaenia 3-angulata, fusco-atrata, glabra, muriculata, 3.5 mm. longa.

Annual; plant yellowish green throughout, stem smooth, striate, sharply angled, erect, 4–7 dm. high, profusely branched at the base with several elongated, decumbent or prostrate branches; stem-leaves thick, smooth, oblong or oblanceolate, rounded or bluntly pointed at the apex, tapering to a short petiole at the base, veins inconspicuous or none except the midrib at the back, 2–5 cm. long, 4–10 mm. wide, often widest above the middle, as long or longer than the internodes, articulate to the foliaceous part of the ocreae; ocreae thin, scarious, with few or no veins, inconspicuous; flowers abundant, 2–8 in the axil of each leaf; perianth segments 6, the outer three sharply carinate, prominently veined, cucullate, green with white edges; style short, 3-parted to the base; stamens 5, yellow; achenes ovate, prominently 3-angled, angles rounded, becoming black, muriculate, 3.5 mm. long, 2 mm. wide.

Specimens examined: The type was collected by Brenckle and Stevens on June 29, 1938, on low ground near a spring adjoining the highway, south of Forsythe. Montana (fig. 2). Specimens (*No. 38–034, Brenckle & Stevens*) are deposited in the Rocky Mountain Herbarium, Laramie, Wyoming; University of Wisconsin Herbarium, Madison; Herbarium of the N. Y. Botanical Garden (TYPE); U. S. National Herbarium, Washington.

This plant is related to *P. ramosissimum* Michx. but differs in the stem, in the manner of branching, in the character and shape of the leaves, and in the early and abundant inflorescence. It differs from *P. latum* Small in the manner of branching, shape and character of leaves and perianth, and by the early bloom.

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[3] Steward, Albert N. *l.c.*: 25, 26.

Polygonum autumnale Brenckle, sp. nov. Annua; caulis erectus, gracilis, 2–5 dm. altus; folia erecta, lanceolata vel linearia, ad apice et base acuminata, 2–4 cm. longa, 2–4 mm. lata, cito decidua; florit aestate sera; perianthi sessiles, ocreis celati; achaenia 3-angulata, anguste ovata, obtuse apiculata, latera plana, fusca, subtiliter punctata, hebetia, 1.6 mm. longa, 0.8 mm. lata.

Annual; stem mostly erect, slender, wiry, terete, finely striate branches erect or spreading below, 2–5 dm. high; spring leaves erect, lanceolate or linear, veined beneath, parallel lined above when dry, pointed at each end, subsessile, pale green, 2–4 cm. long, 2–4 mm. wide, early deciduous, reduced above to linear bracts; ocreae veined, the lower half herbaceous, the upper membranous part evanescent leaving the exposed veins as bristles; inflorescence develops late in summer on terminal branches and twigs, interrupted or contiguous and spike-like; perianth sessile or subsessile, 1–3, mostly hidden in the ocreae, 5-parted, covering the achene; segments green or reddish tinted with white or white and pink margins; achenes obtusely 3-angled, narrowly ovate, obtusely pointed at the top, faces mostly flat or slightly convex, brown, muriculate or minutely striate, dull 1.2–2 mm. long, about .8 mm. wide. Rarely a few blossoms develop in spring.

Specimens examined: The TYPE, *No. 37–32,* collected near Northville, Spink County, South Dakota, September 23, 1937, is deposited in the herbarium of the New York Botanical Garden (fig. 3). The following specimens are in the U. S. National Herbarium.

SOUTH DAKOTA: Rapid City, *D. Griffiths No. 732,* Aug. 29, 1897 (3 sheets). TEXAS: Bell County, *Simon E. Wolff No. 175,* Oct. 17, 1928; Amarillo, *Carlton & Ball No. 1136,* Sept. 15, 1906. MARYLAND: Calvert County, Cheseapeake Beach, *N. D. House No. 1454,* Aug. 20, 1905.

At hand for distribution to those interested are additional specimens of cotype material from South Dakota and North Dakota; Burleigh County, McKensie, *O. A. Stevens No. 485,* Aug. 15, 1940.

This species, practically sterile all summer, has been overlooked or confused with other species. The early loss of the stem leaves and variation in size of all parts according to location, crowding and moisture, make it difficult to present a complete picture of the plant. It has been variously named *P. aviculare, P. prolificum* and *P. leptocarpum,* but from these it differs in the perianths hidden in the ocreae, narrower ripe achene often square-cut on the edges, stub-pointed and mostly less than 2 mm. long, usually from 1.2 mm. to 1.6 mm. long. Late in the season we may find a few exserted achenes which are longer.

The writer wishes to gratefully acknowledge the assistance and advice freely given by Prof. O. A. Stevens of Fargo in preparation of this paper; also to Mr. L. L. Shinners of the University of Wisconsin, Madison, for the Latin diagnoses.

AN UNDESCRIBED LENOPHYLLUM[1] FROM MEXICO

STEPHEN S. WHITE

(WITH ONE FIGURE)

Lenophyllum reflexum White, sp. nov. Folia opposita, late ovata vel elliptica, ad 4.5 cm. longa et 3 cm. lata, acuta, supra plana vel convexa, pleraque reflexa. In vivo folia matura supra purpureo-viridia, infra purpurea, in sicco viridia; juvenile in vivo lucide viridia. Inflorescentia paniculata ramulis tenuibus, siccata rubeo-purpurea. Flores remoti, fere sessiles, bracteis deciduis 3 mm. longis subtenti. Perianthii flavo-virides, siccati saepe rubeo-purpurei. Sepala 4 mm. longa, oblonga, acuta. Petala 6 mm. longa oblanceolata acuta. Stamina 10. Filamenta petala opposita duplices quam longitudine antherae, ad inferiorem tertiam partem petalorum inserta. Carpella 5–6 mm. longa, stylis subulatis, squamis carnosis et truncatis.

Succulent perennial herb. Leaves opposite, broadly ovate to elliptic, up to 4.5 cm. long and 3 cm. wide, acute, flat or convex above, mostly reflexed. Mature leaves on living plant suffused with purple, especially below; young leaves bright green. Inflorescence paniculate, many-flowered, with slender branches, turning reddish-purple when dry. Flowers remote, nearly or quite sessile, subtended by deciduous bracts 3 mm. long. Perianth yellowish-green; sepals 4 mm. long, oblong, acute; petals 6 mm. long, oblanceolate, acute. Stamens 10, the filaments of those opposite the petals becoming twice as long as the anthers, inserted at one-third the height of the petals. Carpels 5–6 mm. long with subulate styles; scales fleshy and truncate.

TYPE in the University of Michigan Herbarium, prepared from a plant grown in the Botanical Gardens of the University of Michigan; collected by *H. H. Bartlett* in 1930 on the Cerro del Diablo, San Carlos Mts., Tamaulipas, Mexico.

This species is clearly distinguished from all other members of the genus by its broad reflexed leaves which are not at all channeled above.

The author wishes to acknowledge his indebtedness to Drs. E. B. Mains and C. L. Lundell of the University of Michigan Herbarium for many valuable suggestions in the preparation of the manuscript.

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[1] Family Crassulaceae.

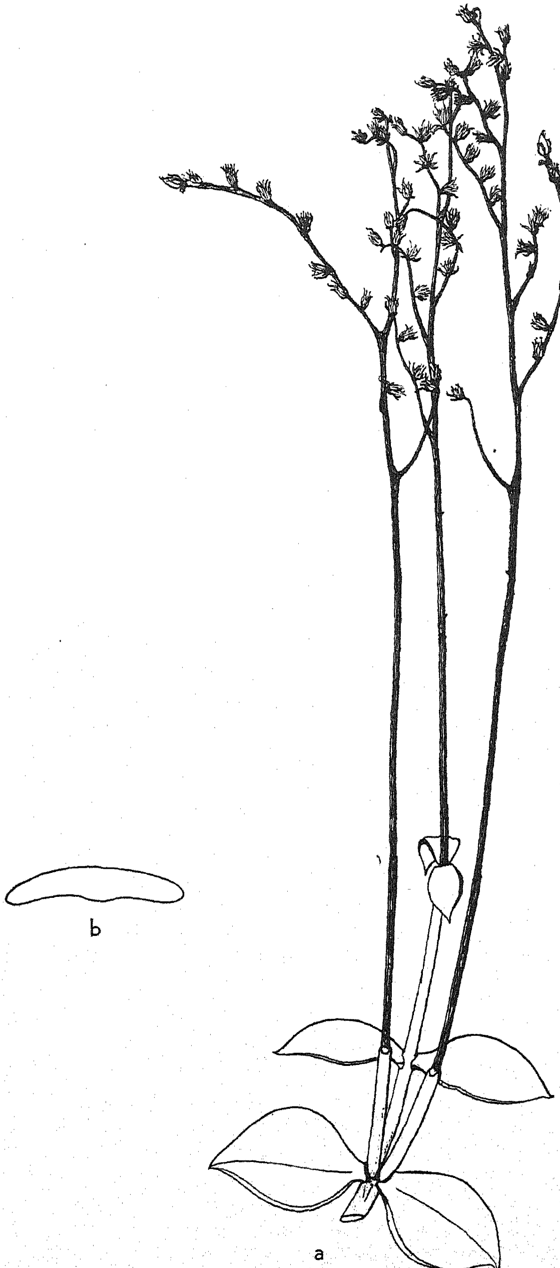

FIG. 1. *Lenophyllum reflexum* White, sp. nov.; *a*, habit, one-half natural size; *b*, cross section of leaf, natural size.

NEW SPECIES AND VARIETIES OF VERBENACEAE FROM CENTRAL AND SOUTH AMERICA

HAROLD N. MOLDENKE

Continued work on the *Verbenaceae* has brought to light a number of as yet undescribed species and varieties from tropical America. It has been thought advisable to place the descriptions of these plants formally on record at this time. Detailed discussions of their relationships and distribution, and complete citation of specimens, will be published at a later date in generic monographs now in preparation.

Bouchea boyacana Moldenke, sp. nov. Herba perennis sublignosa; ramis ramulisque dense puberulis; petiolis crassiusculis complanatis alatis dense puberulis; laminis firme chartaceis ovatis, ad apicem et basim acutis, crasse dentatis utrinque dense adpresso-puberulis; pedunculis rhachideque pedicellisque dense puberulis.

Rather woody perennial; branches and branchlets rather slender, obtusely or subacutely tetragonal, often rather irregular, densely puberulent throughout; nodes not annulate; principal internodes usually abbreviated, 3–15 mm. long; leaves decussate-opposite; petioles rather stout, 1–1.5 cm. long (or less), flattened above and alate from apex to base with a narrow green marginal wing about 1 mm. wide or less, densely puberulent throughout; blades firmly chartaceous, ovate, almost uniformly light-green on both surfaces or somewhat darker above and grayish-green beneath, 1–5 cm. long, 0.5–3.7 cm. wide, acute at apex, coarsely dentate from the widest part to the apex with broadly ovate acute or apiculate antrorse teeth to 7.5 mm. long and 4 mm. wide, acute at base, densely appressed-puberulent on both surfaces, the puberulence often grayish beneath; midrib slender, prominulous on both surfaces; secondaries slender, 2–5 per side, ascending, only slightly arcuate, often extending from near the base to the apex, subprominulous on both surfaces; veinlet reticulation obscure or indiscernible; inflorescence terminal, spicate during anthesis, racemiform in fruit, 4–37 cm. long, many-flowered, erect, the flowers usually imbricate or the lowermost separate; peduncles slender, abbreviated, 1 cm. long or less, along with the rachis densely puberulent; pedicels subobsolete during anthesis or to 1 mm. long, in fruit to 4 mm. long and densely puberulent; foliaceous bracts absent; bractlets and prophylla lanceolate, 1–3 mm. long, attenuate, densely puberulent; calyx tubular, 6–9 mm. long, 1.5–2.5 mm. wide throughout, densely puberulent outside, 5-costate, subhyaline and translucent between the costae, its rim 5-apiculate, the apiculations unequal—four 1–1.5 mm. long and the fifth 0.5–0.9 mm. long, cucullate from within; corolla hypocrateriform, irregular, its tube broadly cylindric, curvate, about 1.5 cm. long, about 1 mm. wide at base, ampliate to 3 mm. somewhat below the apex, glabrous outside, pilose among the stamens within, its limb spreading, 5-parted, 2-lipped, the lobes broadly elliptic, rounded at apex, the largest 6–6.5 mm. long and wide; stamens 4, didynamous, included, inserted about 3 and 4 mm. below the mouth of the corolla-tube, the lower pair shorter; filaments filiform, about

1.4 and 2.4 mm. long, glabrous or the larger pair obscurely pilose; anthers broadly ovate-elliptic, about 1 mm. long and wide, the connective ovate-triangular; pistil included; style capillary, about 9 mm. long, glabrous; stigma 2-lobed, the anterior lobe club-shaped and erecto-recurved, the posterior lobe minute and tooth-like; ovary elongate-oblong, about 2.5 mm. long and 1 mm. wide, glabrous.

COLOMBIA—BOYACÁ: Cordillera Oriental, Soatá, arid slopes, alt. 2130 m., *J. Cuatrecasas 1017*, September 6, 1938, TYPE; in the Britton Herbarium at the New York Botanical Garden.

Duranta armata Moldenke, sp. nov. Frutex; ramis ramulisque rigidis sarmentosis spinosis adpresso-puberulis glabrescentibus; foliis fasciculatis numerosis subsessilibus vel brevissime petiolatis; laminis chartaceis oblanceolatis vel ellipticis acutis vel obtusis vel rotundatis integris vel 2–4-dentatis, ad basim acutis vel attenuatis, utrinque sparse minuteque puberulis glabrescentibus, supra nitidis, subtus punctatis; inflorescentiis abbreviatis terminalibus 1- vel pauci-floris.

Spiny shrub; branches and branchlets medium-slender, stiff, twiggy, obtusely tetragonal or subterete (sharply tetragonal when young), rather densely appressed-puberulent when young, glabrescent in age, viciously spinose; spines numerous, slender to very stout, alternate-scattered, rarely opposite or ternate, 0.9–3.3 cm. long, very stiff and sharp-pointed, unbranched, often bearing an opposite pair of buds at about the middle, glabrous and shiny; nodes not annulate; principal internodes abbreviated, 1–2 cm. long or less; leaves borne in fascicles on very much abbreviated spur-like twigs subtending the spines, numerous, subsessile or very short-petiolate; petioles slender, 1–3 mm. long or obsolete, appressed-puberulent, submargined; blades chartaceous, oblanceolate or elliptic, 0.4–3 cm. long, 4–14 mm. wide, varying from acute (on large leaves) to obtuse or rounded (on small leaves) at apex and often subemarginate, entire or with 1 or 2 appressed irregular teeth on each margin near the apex, acute or attenuate at base, sparsely and minutely puberulent on both surfaces when young, glabrous in age and shiny above and punctate beneath; midrib slender, flat or subimpressed above, prominulous beneath; secondaries slender, 2–5 per side, flat or subimpressed above, usually flat beneath; veinlet reticulation obscure or indiscernible; inflorescence reduced, terminating the branchlets and twigs, racemiform, 1–few-flowered, 1–5.5 cm. long; peduncles slender, sharply tetragonal, abbreviated, 2–18 mm. long, along with the rachis rather densely appressed puberulent; pedicels slender, about 1 mm. long, elongate to 4 mm. in fruit, puberulent; bractlets varying from linear to spatulate, stipitate, 1–4 mm. long, puberulent; calyx campanulate, 3–3.5 mm. long, 2.5–3 mm. wide at apex, 5-costate, appressed-puberulent outside, its rim truncate, shortly 5-apiculate; corolla blue, hypocrateriform, its tube broadly cylindric, about 7 mm. long, glabrous outside except at the very apex, straight or slightly curved, its limb 5-parted, 7–10 mm. in diameter, densely pulverulent-puberulent on both surfaces; fruiting-calyx broadly campanulate, papery, obvolute and subincluding the fruit, eventually splitting, minutely puberulent or glabrate and shiny, its rim usually persistently whitish puberulent-pilose; fruit tetragonal, about 4 mm long and wide, very distinctly 4-lobed and -sulcate in drying, glabrous and shiny.

PERU—CUZCO: Upa Blanca, near Cuzco, alt. 3400–3600 m., *Fortunato L. Herrera 85*, TYPE; in the herbarium of the Botanisches Museum at Berlin, received there in February, 1923.

Duranta Dombeyana Moldenke, Prelim. Alph. List Invalid Names 25, hyponym (1940), sp. nov. Frutex; ramis glabratis saepe sparse spinosis; ramulis dense fulvo-tomentosis; foliis oppositis; petiolis dense tomentosis glabrescentibus; laminis chartaceis ellipticis, ad apicem obtusis vel acutis vel subacuminatis, ad basim rotundatis vel acutis vel acuminatis, integris vel irregulariter serratis, supra sparse breviterque pubescentibus vel puberulis glabrescentibus, subtus dense adpresso-tomentosis; inflorescentiis axillaribus terminalibusque; floribus secundis; pedunculis rhachideque dense flavescento-tomentosis.

Strict shrub, 2–4 m. tall; branches rather slender, obtusely tetragonal, glabrate, sometimes sparsely spinose; spines axillary, opposite, stout at base, sharply pointed at apex, 5–7 mm. long; branchlets slender, obtusely tetragonal, densely fulvous-tomentose with short appressed tomentum; nodes not annulate; principal internodes 0.5–4 cm. long, those on the twigs extremely abbreviated; leaves decussate-opposite, often with an additional pair or a fascicle borne on an extremely abbreviated twig in the axil; leaf-scars corky, prominent, semicircular; petioles slender, 4–8 mm. long, margined above, densely tomentose or glabrescent; blades chartaceous, rather uniformly dark-green above or slightly lighter beneath, sometimes brunnescent above in drying, elliptic, 1.7–9.3 cm. long, 1.1–4 cm. wide, varying from obtuse to acute or even subacuminate (occasionally emarginate) at apex, entire or rarely rather irregularly serrate just below the apex or from the widest part to the apex with sharp-pointed antrorse teeth, varying from rounded to acute or acuminate at base and usually more or less prolonged into the petiole, lightly short-pubescent or puberulent above, glabrescent in age, densely appressed-tomentose with fulvous or yellowish hairs beneath; midrib slender, flat or subimpressed above, prominent beneath; secondaries slender, 4–6 per side, ascending, not much arcuate, flat or subimpressed above, prominulous beneath, joined in many loops near the margins; veinlet reticulation sparse, the larger portions subimpressed above and subprominulous beneath, the rest obscure or indiscernible; inflorescence axillary and terminal, the axillary ones 3–7 cm. long, the terminal one to 20 cm. long, spicate or subracemiform, many-flowered, the flowers secund; peduncles abbreviated, 4–13 mm. long, along with the rachis densely flavescent-tomentose; pedicels obsolete or to 2.5 mm. long and densely flavescent-tomentose; bractlets and prophylla linear, 1–6 mm. long, densely tomentose, caducous; calyx campanulate, 3–4 mm. long, 2–3.5 mm. wide, 5-costate, densely flavescent-tomentose outside, its rim truncate, very obscurely and minutely 5-apiculate; corolla hypocrateriform, its tube broadly cylindric, curved, 1.3–1.4 cm. long, glabrous outside below the bend, puberulent above, its limb 8–11 mm. in diameter, densely puberulent on both surfaces; fruiting-calyx obvolute and rostrate, completely enclosing the fruit, firm, nigrescent, short-pubescent with canescent hairs (especially on the apical beak), becoming glabrous and shiny in age, eventually splitting; fruit subglobose, to 1 cm. long and wide, glabrous, shiny, nigrescent in drying, umbonate-rostrate at apex.

ECUADOR: between Loja and Portovelo, *Joseph Nelson Rose, Abelardo*

Pachano, & George Munson Rose 23,347, October 3–6, 1918, TYPE; in the Britton Herbarium at the New York Botanical Garden.

Duranta guatemalensis Moldenke, sp. nov. Frutex; ramis ramulisque spinosis dense adpresso-tomentosis glabrescentibus; foliis oppositis vel suboppositis plerumque fasciculatis; petiolis dense tomentoso-pubescentibus glabrescentibus; laminis tenuiter chartaceis vel submembranaceis oblanceolato-ellipticis vel ellipticis, ad apicem obtusis vel rotundatis, integris vel sparse serratis, supra parce pilosulis glabrescentibus, subtus puberulento-pilosulis; inflorescentiis axillaribus terminalibusque; pedunculis rhachideque dense adpresso-tomentosis.

Spiny shrub; branches and branchlets slender, obtusely tetragonal or subterete, densely appressed-tomentose with white or sordid tomentum when young, glabrescent in age; spines in opposite or subopposite pairs, stiff, slender, 2.5–14 mm. long, glabrous, sharp-pointed; nodes not annulate; principal internodes 1–3.7 cm. long; buds densely tomentose; leaves decussate-opposite or subopposite, often with additional fascicles on extremely abbreviated twigs in their axils; petioles very slender, 1–5 mm. long, densely tomentose-pubescent with appressed sordid hairs, glabrescent in age; blades thin-chartaceous or submembranous, oblanceolate-elliptic or elliptic, lighter beneath, 1.2–4 cm. long, 8–16 mm. wide, obtuse or rounded at apex, entire or sparsely serrate at or near the apex with a few, appressed, mostly rounded teeth, sparsely pilosulous above, glabrescent in age, rather sparsely puberulent-pilosulous beneath (somewhat more densely so on the larger venation); midrib very slender, flat or subimpressed above, flat or prominulous beneath; secondaries very slender, 3–5 per side, ascending, not much arcuate, flat or subimpressed above, flat or prominulous beneath, obscurely joined at the margins beneath; veinlet reticulation sparse, mostly indiscernible above and obscure beneath; inflorescence axillary and terminal, racemiform, 3–5 cm. long, many-flowered; peduncles very slender, 3–6 mm. long, along with the slender rachis densely appressed-tomentose like the branchlets; bracts and prophylla linear, 1–2 mm. long, densely tomentose, deciduous; calyx tubular, 5–7.5 mm. long, 2–3.5 mm. wide, densely or irregularly short-pubescent-pilose outside, less so in age, 5-costate, thin-textured between the ribs, its rim truncate and very minutely 5-apiculate; corolla hypocrateriform, its tube broadly cylindric, slightly curved, 7–10 mm. long, subglabrate below outside, densely puberulent toward the apex, its limb 5-parted, 9–11 mm. in diameter, very densely appressed-puberulent with canescent hairs on both surfaces.

GUATEMALA—QUICHÉ: Chiul, alt. 2600 m., *Enrique Teófilo Heyde & Ernesto Lux 2947*, in June 1892, TYPE; in the Gray Herbarium of Harvard University.

Duranta peruviana Moldenke, sp. nov. Frutex; ramis ramulisque dense breviterque pubescentibus glabrescentibus, ad nodos decussato-complanatis, saepe spinosis; foliis oppositis; petiolis dense breviterque incano-pubescentibus; laminis tenuiter chartaceis ellipticis, ad apicem acutis vel breviter acuminatis, integris vel serratis, supra dense puberulis, subtus dense velutino-pubescentibus; inflorescentiis axillaribus terminalibusque saepe paniculatis; pedunculis rhachideque dense breviterque incano-pubescentibus.

Shrub; branches and branchlets slender, obtusely or subacutely tetragonal, decussately flattened at the nodes, densely short-pubescent when young, glabrescent in age, grayish, sometimes bearing a few pairs of short blunt spines above the nodes; nodes not annulate, mostly flattened and somewhat ampliate; principal internodes 2–4 cm. long; leaves decussate-opposite; petioles slender, 4–10 mm. long, densely short-pubescent with incanous hair; blades thin-chartaceous, uniformly dark-green on both surfaces, elliptic, 1.3–7 cm. long, 0.8–4.5 cm. wide, acute or short-acuminate at apex, entire or serrate with blunt appressed teeth from below the middle to the apex, densely puberulent above, densely velutinous-pubescent with sordid-grayish hair beneath; midrib slender, flat or subimpressed above, prominent beneath; secondaries very slender, 6–9 per side, arcuate-ascending, flat or subimpressed above, prominulous beneath; veinlet reticulation obscure or indiscernible above, often obscure beneath; inflorescence axillary and terminal, racemiform or paniculate, 7–14 cm. long, often bearing 1 or more pairs of opposite racemiform branches; racemes many-flowered, spreading; peduncles slender, 0.5–2.5 cm. long, usually abbreviated, along with the slender rachis densely short-pubescent with incanous hairs; pedicels very slender, obsolete or to 3 mm. long during anthesis and fruit, densely incanous-pubescent; calyx tubular-campanulate, 3.5–4 mm. long, about 2 mm. wide, 5-costate, densely strigose-pubescent with incanous hair, its rim truncate, minutely 5-apiculate; corolla hypocrateriform, its tube slightly curved, 6–8 mm. long, densely puberulent outside above the calyx, its limb 5-parted, to 1 cm. in diameter, densely incanous-puberulent on both surfaces.

PERU—CUZCO: between Santa Rosa and Quillabamba, Convención, *J. Soukup 825*, in January, 1938, TYPE; in the herbarium of the Field Museum of Natural History at Chicago.

DURANTA PERUVIANA var. **longipedicellata** Moldenke, var. nov. Haec varietas a forma typica speciei recedit pedicellis post anthesin usque ad 8 mm. longis, floribus nutantibus, ramulis foliisque sparsiore pubescentibus.

This variety differs from the typical form of the species in its pedicels being up to 8 mm. long after anthesis, the flowers nutant, and the branchlets and lower leaf-surfaces less densely velutinous-pubescent.

PERU—CUZCO: valley of the Urubamba, Machupicchu, alt. 2200 m., *Fortunato L. Herrera 3209*, in October, 1931, TYPE; in the herbarium of the Field Museum of Natural History at Chicago.

Duranta Skottsbergiana Moldenke, Suppl. List Vern. Names 10, hyponym (1940), sp. nov. Frutex vel arbor parva; ramis plerumque spinosissimis glabratis; ramulis dense breviterque pubescentibus glabrescentibus saepe spinosis; foliis oppositis vel ternatis vel irregulariter dispositis, saepe fasciculatis; petiolis marginatis breviter pubescentibus glabrescentibus; foliis subcoriaceis nitidis ellipticis vel lanceolatis vel oblanceolatis, ad apicem obtusis vel acutis vel subemarginatis, ad basim acutis vel acuminatis, integris vel sparse arguteque serratis, supra sparse pilosis glabrescentibus, subtus dense adpresso-pubescentibus dein glabrescentibus et impresso-punctatis; inflorescentiis axillaribus terminalibusque saepe paniculatis.

Shrub or small tree, to 6.5 m. tall; branches medium-stout, brown, subterete, glabrate, prominently lenticellate-verruculose, usually very spinose; branchlets medium, stiff, densely short-pubescent when young, glabrescent in age, often spinose, subterete or angular; spines very stiff, rather slender, 0.6–3.4 cm. long, very sharp-pointed, gray, glabrous, opposite, ternate, or scattered; nodes not annulate, often triangular-flattened on younger parts; principal internodes 1–5 cm. long; leaves opposite, ternate, or scattered (on older branches), often borne in fascicles on greatly abbreviated twigs from below the spines on older wood; petioles slender, 2–11 mm. long, densely or sparsely short-pubescent, glabrescent in age, margined from apex to base, flat above; blades subcoriaceous, dark-green above, lighter beneath, shiny on both surfaces, mostly elliptic, varying to lanceolate or oblanceolate, 1.5–4.5 cm. long, 0.6–2.7 cm. wide, obtuse or acute at apex, varying to subemarginate, entire or sparsely sharp-serrate with appressed teeth toward the apex, acute or acuminate at base, often attenuate into the petiole, sparsely scattered-pilose above when young, soon glabrescent, densely appressed-pubescent beneath when young, eventually glabrous and impressed-punctate; midrib slender, flat above, prominent beneath; secondaries slender, 4–6 per side, arcuate-ascending, flat above, sharply prominent beneath, not anastomosing; veinlet reticulation sparse, obscure on both surfaces or indiscernible in mature leaves; inflorescence racemiform or paniculate, axillary and terminal, 2–19 cm. long, often bearing one or more pairs of racemiform branches near the base, arcuately ascending or recurved, many-flowered; flowers subsecund; bracts large and foliaceous, resembling the leaves in all respects but smaller, a pair subtending each pair of inflorescence-branches; bractlets elliptic or spatulate, stipitate, to 7 mm. long and 3 mm. wide, densely short-pubescent, borne near the base of the racemes, caducous; prophylla linear, minute, about 1 mm. long, densely pubescent; peduncles slender, 1–2 cm. long or more abbreviated, along with the slender rachis densely short-pubescent, glabrescent in age; calyx campanulate, 4–5 mm. long, 2.1–4 mm. wide, 5-costate, thin-textured between the ribs, densely puberulent or short-pubescent with appressed cinereous hairs, its rim truncate, minutely 5-apiculate; corolla hypocrateriform, pale-lilac, pale-blue, or lavender, its tube broadly cylindric, 1–1.4 cm. long, curved, the uppermost 3–4 mm. densely puberulent outside, the remainder glabrous outside, its limb 5-parted, 7–10 mm. in diameter, densely cinereous-puberulent on both surfaces; fruiting-calyx leathery, glabrate; fruit subglobose, yellow, about 1 cm. long and wide.

PERU: Mito, in sunny stream canyons, alt. about 3000 m., *J. Francis Macbride & Featherstone 1484*, July 8–22, 1922, TYPE; in the herbarium of the Field Museum of Natural History at Chicago.

This species is named in honor and appreciation of my respected colleague, Dr. Carl Skottsberg, Director of the Botanical Garden at Göteborg, Sweden, to whose boundless energy and inexhaustible courage this garden will always be a lasting memorial, and who has found time, amid all his administrative work, to do such noteworthy botanical exploration in Chile, the Galapagos Islands, Hawaii, and elsewhere.

Duranta Woronowii Moldenke, sp. nov. Frutex vel arbor; ramulis glabris inermibus; foliis oppositis vel suboppositis; petiolis debilibus minute obscureque puberulis vel subglabratis; laminis tenuiter chartaceis vel submembranaceis brunnescentibus anguste ellipticis, ad apicem acutis, ad basim cuneato-attenuatis vel subacuminatis, integris, utrinque minutissime obscureque subpilosulis glabrescentibus; inflorescentiis axillaribus terminalibusque racemiformibus; floribus non secundis plusminus erectis; pedunculis glabris.

Shrub or tree; branchlets slender, dark, obtusely tetragonal, lenticellate, glabrous, unarmed; nodes not annulate, not ampliate; principal internodes 2.5–3.5 cm. long; leaves decussate-opposite or subopposite; petioles slender, weak, 5–10 mm. long, minutely and obscurely puberulent or subglabrate, canaliculate above; blades thin-chartaceous or submembranous, dark-green above, lighter beneath, brunnescent in drying, narrow-elliptic, 4.5–8 cm. long, 1.2–2.5 cm. wide, acute at apex, entire, cuneate-attenuate or subacuminate at base, very minutely and obscurely subpilosulous on both surfaces or glabrescent; midrib slender, flat above, prominulous beneath; secondaries slender, 5–7 per side, mostly flat on both surfaces, often obscure above, arcuate-ascending, indistinctly joined at the margins beneath; veinlet reticulation fine, mostly indiscernible above; inflorescence axillary and terminal, racemiform, 3–17 cm. long, many-flowered, the axillary ones confined to a pair in the uppermost axils; flowers not secund, more or less erect; peduncles slender, dark, 0.8–2.8 cm. long, glabrous; rachis slender, dark, glabrous or very slightly puberulent-pilose with obscure and scattered minute hairs; pedicels slender, 1–2 mm. long, very densely strigose-puberulent with incanous hairs, elongate to 6 mm. in fruit, usually erect; bractlets stipitate, linear or oblong, 3–9 mm. long, rather conspicuous, minutely pilose, long-persistent; calyx campanulate, about 2.5 mm. long, rather densely appressed-strigillose or puberulent with incanous hair, 1.5–2 mm. wide, indistinctly costate, its rim truncate, very minutely and obscurely 5-apiculate; corolla hypocrateriform, its tube 4.5–6 mm. long, rather narrow-cylindric, straight or curved, the lower portion glabrous outside, the upper portion densely appressed pulverulent-puberulent, its limb 5-parted, about 5 mm. in diameter, densely pulverulent-puberulent on both surfaces; fruiting-calyx enlarged, leathery, nigrescent in drying. obscurely appressed-puberulent or glabrescent, obvolute, including the (immature?) fruit, not beaked.

COLOMBIA—TERRITORIO DEL CAQUETÁ: Rio Caquetá, Tres Esquinas, *Georg N. Woronow & S. Juzepczuk 6243*, July 22, 1926, TYPE; in the herbarium of the Field Museum of Natural History at Chicago. Named in honor of G. N. Woronow.

Ghinia Cardenasi Moldenke, Geogr. Distrib. 28, nom. nud. (1939), sp. nov. Herba sublignosa; ramis acute tetragonis costatis densissime puberulis; nodis annulatis; petiolis densissime puberulis; laminis chartaceis ovatis vel rare ellipticis argute serratis, ad basim abrupte acutis vel subtruncatis, utrinque plusminus puberulis vel supra subglabratis; inflorescentiis axillaribus spicatis; pedunculis rhachideque densiuscule incano-puberulis tetragonis costatis.

Herb, about 50 cm. tall, woody at base; branches slender, acutely tetragonal, very densely puberulent throughout, longitudinally ribbed; nodes annulate, not ampliate; principal internodes 1–3.5 cm. long; leaves decussate-opposite; petioles slender, 3–6 mm. long, very densely puberulent like the branchlets; blades chartaceous, rather uniformly green on both surfaces or somewhat lighter beneath, ovate or rarely elliptic, 1.5–3.5 cm. long, 0.8–2 cm. wide, obtuse (in outline) at apex, sharply serrate from almost the base to the apex with acute antrorse teeth, abruptly acute or subtruncate at base, densely puberulent above and densely canescent beneath when young, very obscurely puberulent or subglabrate above in age, more plainly puberulent beneath; midrib slender, subimpressed above, prominulous beneath; secondaries slender, 6–8 or more per side, close together, subparallel, straight and ascending, mostly extending direct to the sinuses between the teeth and secondarily into the teeth themselves, mostly subimpressed above, prominulous beneath; veinlet reticulation sparse, obscure on both surfaces; inflorescence axillary, spicate, 4.5–18 cm. long, many-flowered, the flowers during anthesis barely overlapping, the lowermost separate; peduncles (3–5 cm. long) and rachis slender, rather densely incanous-puberulent throughout, tetragonal and costate; pedicels obsolete; bractlets linear or filiform, 3–4 mm. long, puberulent; calyx tubular, 4–5 mm. long, 1–1.5 mm. wide, 5-costate, hyaline between the ribs, densely incanous-puberulent, its rim 5-apiculate, the apiculations filiform and 1–1.5 mm. long; corolla hypocrateriform, lilac, its tube cylindric, curved, 5–7 mm. long, its limb 5–7 mm. in diameter; fruiting-calyx spreading-campanulate, about 6 mm. long and to 6 mm. in diameter, appressed-puberulent, its rim scalloped and long-apiculate, the apiculations filiform and about 2 mm. long; fruit obovate, the body about 6 mm. long and 5 mm. wide, glabrous, prominently reticulate at apex, with 3 divergent horns to 4 mm. long, sharp-pointed and spine-like.

BOLIVIA—SANTA CRUZ: Ipias—Chiquitos, in grassy pampas, alt. 230 m. *Martin Cárdenas 2946,* in October, 1934, TYPE; in the herbarium of the Field Museum of Natural History at Chicago.

Lantana boyacana Moldenke, sp. nov. Frutex; ramis ramulisque densiuscule puberulis et patenti-pilosis glabrescentibus; nodis annulatis; foliis oppositis; petiolis plusminus marginatis dense adpresso-puberulis et patenti-pilosis; laminis chartaceis lanceolatis vel ovatis, ad apicem acutis vel subacutis, regulariter crenato-serrulatis utrinque dense velutino-puberulentibus et parce longeque pilosis, supra plerumque subbullatis; bracteolis magnis foliaceis ellipticis vel ovatis vel obovatis.

Shrub; branches and branchlets slender, obscurely tetragonal or subterete, rather more plainly tetragonal when young, rather densely puberulent and also spreading-pilose with cinereous hair, glabrescent in age; nodes annulate; principal internodes 0.6–5.8 cm. long; leaves decussate-opposite; petioles slender, 4–10 mm. long, more or less margined (especially toward the apex), densely appressed-puberulent and spreading-pilose with cinereous hair, the long pilose hairs abundant and 2 or 3 times as long as the puberulent ones; blades chartaceous, gray-green on both surfaces, lighter beneath, lanceolate or ovate, 1.7–5 cm. long, 1.1–3.5 cm. wide, acute or subacute at apex, regularly crenate-serrulate along the whole margins except at the very base with rounded, appressed, minute teeth, densely velutinous-puberulent with grayish or sordid hair on both surfaces, interspersed with much longer pilose hairs on the larger venation, often subbullate above; midrib slender, flat above, prominulous beneath; secondaries slender, 5–8 per side, arcuate-ascending, rather straight and not much arcuate, flat or subimpressed above, prominulous beneath; vein and veinlet reticulation abundant, mostly more or less impressed above, flat or prominulous beneath; inflorescence axillary, capitate; peduncles slender, 2.5–6.5 cm. long, rather densely incanous-puberulent and long-pilose like the branchlets; heads hemispheric, 1.5–2.5 cm. wide, densely many-flowered; involucral bractlets large and conspicuous, foliaceous, elliptic, ovate, or obovate, the lowermost ones 5–11 mm. long, 2.5–7.5 mm. wide, sessile, acute or abruptly short-acuminate at apex, densely short-pubescent on both surfaces with substrigose incanous hair; receptacle to 6 mm. long; corolla about 7 mm. long, its limb about 4 mm. wide.

COLOMBIA—BOYACÁ: Valle de la Uvita, woods and thickets near Uvita, alt. 2490–2560 m., *J. Cuatrecasas 1851*, September 16, 1938, TYPE; in the herbarium of the Instituto Botanico, Bogotá, Colombia.

Lantana soatensis Moldenke, sp. nov. Frutex; ramis ramulisque gracillimis dense albido-strigosis subglabrescentibus; nodis annulatis; foliis oppositis numerosis saepe fasciculatis; petiolis dense albido-strigosis; foliis chartaceis ellipticis vel ovatis, ad apicem acutis, ad basim acuminatis, argute serrulatis utrinque dense sericeo-strigosis; bracteolis ovatis.

Shrub; branches and branchlets very slender, gray, obtusely tetragonal, densely strigose with short and appressed white hair, less densely so or even glabrescent in age; nodes annulate on young branchlets, less plainly so on older ones; principal internodes 0.5–6 cm. long; leaves decussate-opposite, abundant, often bearing additional fascicles on much abbreviated twigs in their axils; petioles slender, 3–6 mm. long, densely strigose with white hair like the branchlets; blades chartaceous, elliptic or ovate, 0.6–2.5 cm. long, 0.4–1.6 cm. wide, acute at apex, sharply serrulate from the widest part to the apex, acuminate at base, densely sericeous-strigose on both surfaces with white antrorse closely appressed hair, more densely so on the larger venation beneath; midrib slender, subimpressed above, prominulous beneath; secondaries very slender, 4–6 per side, arcuate-ascending, subimpressed above, prominulous beneath; veinlet reticulation obscure or indiscernible on both surfaces; inflorescence axillary, capitate; peduncles very slender, 1–2.5 cm. long, densely white-strigose like the branchlets; heads ovate-elongate, to 1 cm. wide and 1.5 cm. long, densely many-flowered; involucral bractlets ovate, sessile, the lowermost to 6 mm. long and 3 mm. wide, sharply acute at apex, densely white-strigose on both surfaces; corolla about 5 mm. long.

COLOMBIA—BOYACÁ: Soatá, arid slopes, alt. 2130 m., *J. Cuatrecasas 1031*, September 6, 1938, TYPE; in the United States National Hebarium at Washington.

THE NEW YORK BOTANICAL GARDEN,
NEW YORK, NEW YORK.

INDEX TO AMERICAN BOTANICAL LITERATURE

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

Papers that relate exclusively to bacteriology, forestry, agriculture, horticulture, manufactured products of vegetable origin, or laboratory methods are not included. If users of the Index will call the attention of the editor to errors or omissions, their kindness will be appreciated.

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RELATION OF TEMPERATURE TO THE ASCORBIC ACID CONTENT OF COWPEA PLANTS

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(WITH FIVE FIGURES)

Few investigations on the relation of temperature to the synthesis and accumulation of ascorbic acid have been reported and brief mention only (Reid 1941) has been made of its influence on metabolic losses of the vitamin in intact plants. Most of these reports have dealt with the effect of temperature on the percentage content of the vitamin at some particular stage of development. There is no previous work showing its effect on the total quantity of ascorbic acid at different stages of development.

Kuthy (1938) as a result of experiments with wheat, barley, oats, and corn stated that more ascorbic acid is formed at 15° than at 10° C. Povolockajà (1937a) found that a lowering of temperature retards germination and growth and tends to increase the vitamin C concentration. This was noted particularly in legumes. He found (1937a) that the rate of accumulation of vitamin C varies with the rate of respiration and concluded that the relation is not fortuitous but a causal one. Moldtmann (1939) germinated seeds of several different types in darkness at different temperatures and determined the ascorbic acid content when they had attained approximately the same size. The highest ascorbic acid values expressed as milligrams per cent was found in *Pisum sativum* and *Avena sativa* grown at relatively low temperatures (3° C.) and decreasing values toward a high temperature (30° C.). In *Zea mays* there was a slightly higher content at the higher temperatures than at 10° C. and in *Polygonum fagopyrum* definitely higher at 25° than in the lower temperatures employed (5° to 15°). There was no difference in the ascorbic acid content of *Vicia faba* at 5, 10, and 25° and in *Phaseolus vulgaris* a higher content at 10 and 15° than at 5 and 25° was found. Moldtmann concluded from his results that there is no agreement between germination temperature and the ascorbic acid content, —that the temperature which is most favorable for ascorbic acid synthesis varies in the different types. In tests with *Vicia faba* and *Pisum sativum* he reported that differences in temperature caused no change or only a slight

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change in ascorbic acid content but that relatively high temperatures definitely favored respiratory intensity.

Wolf (1938) studied the variations in the percentage content of ascorbic acid in detached leaves of *Bryophyllum calycinum* when kept in darkness at different temperatures. At 20° C. the ascorbic acid content quickly decreased, whereas at 7 and 37° it had decreased little after 48 hours in darkness.

PROCEDURE

To determine the relation of temperature to ascorbic acid accumulation and growth, studies were conducted with young plants grown at different temperatures,[1] some in darkness and others in light. Seeds of uniform size were planted in washed white sand contained in glazed crocks of the shallow type. The cultures, containing twenty-five plants each, were kept uniformly moist with tap water. Tests were conducted with three groups of plants grown in darkness, one at 22°, another at 26°, and a third at 29° C. A humidity of approximately 80 per cent was maintained at each of the three temperatures. Four cultures, grown at each temperature were used in making daily determinations of the green weights, dry weights, and ascorbic acid content. With the indophenol method duplicate ascorbic acid assays were made, ten plants being used in each. Forty plants were used in each of the dry weight determinations. Similar tests were conducted with plants grown in daylight in the greenhouse, some at 24°, others at 29° C. Tests were conducted with and without the addition of nutrient solutions.

OBSERVATIONS

Experiments with Seedlings Grown in Darkness. The maximum ascorbic acid values were lower but were reached earlier in the plants grown at 29° than in those grown at 26 or 22°. In one of the tests there was very little difference between the maximum at the two latter temperatures but in both tests those at 26° were reached earlier than those at 22°. There was little difference in the rate of increase at the two higher temperatures during the first four days, whereas at the lower temperature the rate was definitely lower. The maximum green weight was not attained until two days later than the maximum ascorbic values in each of the three groups of plants. The maximum green weight differences may be significant but the variations in different tests were not always in this order and were probably caused by slight differences in the original weights of the seeds used in different cultures. The total fresh weight and ascorbic acid values per plant at successive stages of growth in darkness under each of the three temperatures are shown in figure 1. The ascorbic acid curves have three phases: one, a period of very rapid accumulation at the two higher temperatures and somewhat less so at the lower, another of less rapid increase when the reserves in the cotyledons are nearing exhaustion, followed by a period of loss.

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[1] Temperature chambers in the Cold Storage Laboratory of the Division of Fruit and Vegetable Crops and Diseases, U.S.D.A., were employed in these experiments.

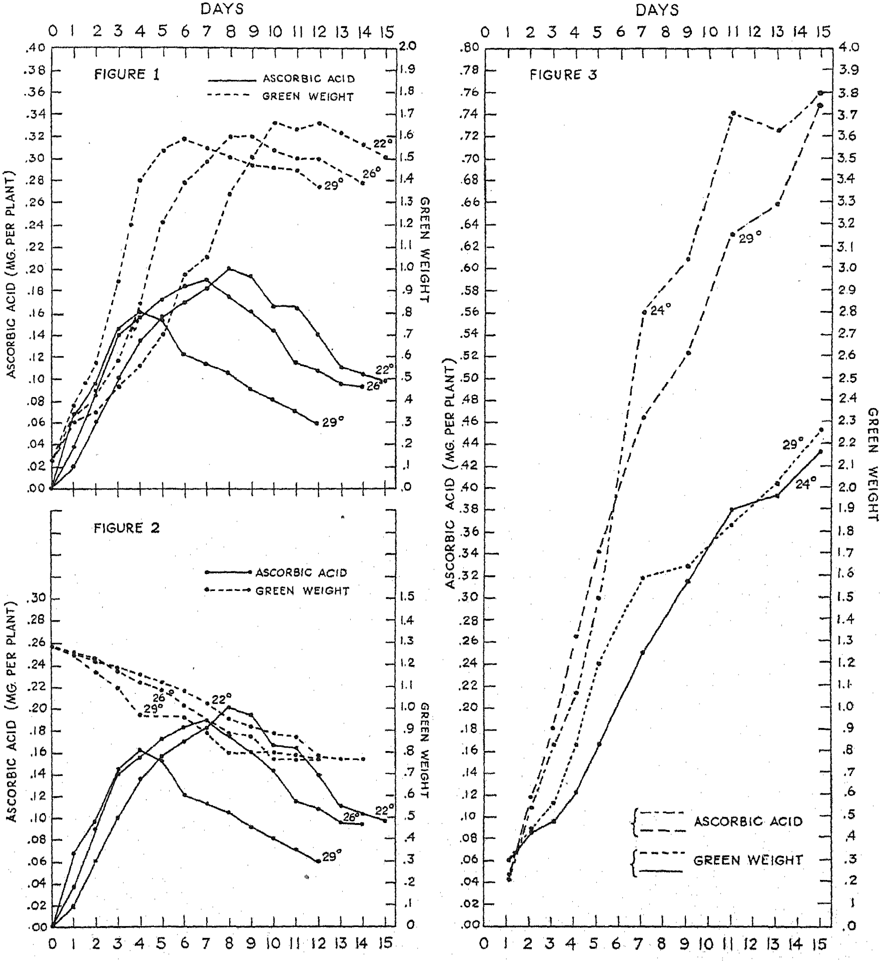

FIG. 1. Ascorbic acid (mg. per plant) and green weights (g.) of seedlings grown in darkness at different temperatures. FIG. 2. Ascorbic acid (mg. per plant) and dry weights (g. × 10) of seedlings grown in darkness at different temperatures. FIG. 3. Green weight (g.) and ascorbic acid content (mg.) of seedlings grown in light at 29° and 24° C.

Separate ascorbic acid and green weight determinations of the different organs were made. No marked differences in either the green weight or ascorbic acid values of the hypocotyls or epicotyls of seedlings grown at different temperatures were found. The primary leaves attained the greatest weight at 29°, but little difference was found between those grown at the other two temperatures. The maximum ascorbic acid values in the leaves of 10 seedlings was 0.59, 0.54, and 0.49 milligrams at 29, 26, and 22° respectively. In contrast, in the roots the maximum green weights were 3.1, 4.0, and 3.9 grams and the ascorbic acid values were 0.41, 0.80, and 0.77 milligrams at the high, medium, and low temperatures respectively.

The most rapid synthesis of ascorbic acid from the food reserves in the cotyledons and the most rapid depletion of the reserves as evidenced by a visible loss of plumpness and a decrease in dry weight were observed at 29°. This may be noted in the appearance of the cotyledons of five-day-old plants at each of the three temperatures as shown in figure 4.[2] The maximum ascorbic acid values were observed in the cotyledons at 29° after 24 hours, at 26° after 48 hours, thereafter decreasing in both sets. At 22° the maximum value was found after two days and was maintained at approximately the same level until the fourth day. Shedding of most of the cotyledons occurred by the sixth, eighth, and tenth days at 29, 26, and 22° respectively.

The effect of temperature on rapidity of decrease in dry weight at successive stages of development is shown in figure 2. The dry weights continued to decrease for approximately two days after the total green weights ceased to increase. During this period growth continued as measured by the increasing length of the stems (epicotyls). Loss in fresh weight of the hypocotyls at this stage was responsible for the lack of increase in total green weight. The results tend to show that the final dry weight is approximately the same in plants grown at the three temperatures, suggesting that although the rate of respiration varied, the total amount of respiration was approximately the same.

Experiments with Plants Grown in Light. These experiments were conducted during the winter months when carbohydrate synthesis was greatly limited by the low light intensity and also by the short daily periods of illumination. With the restricted carbohydrate supply only a slight effect on growth resulted from the addition of mineral nutrients.

Results of the tests with plants grown without added nutrients are shown in tables 1 and 2, and figure 3 shows graphically the differences in total green weight and ascorbic acid values at successive stages of development of plants grown at 24° and at 29° C. It was not possible to maintain a fairly uniform temperature at a level lower than 24° in this test. During the first two days of the experimental period the temperature was approximately 29° for the two groups of plants. Between the second and third days, following the shifting of half of the plants to a temperature of 24°, differences in the growth rate were observed. This was at the time the plants were beginning to emerge above the sand. It has been shown previously (Reid 1938) that the most rapid development of the mesophyll tissue and of increase in total ascorbic acid in the leaves of cowpea plants grown in the light at 29° C. occurs between the third and fifth days. In the entire plant the rapid rate of gain in the total content of vitamin C continues until the sixth to the

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[2] The leaves of the plants, especially those of the plant grown at 26°, became somewhat green during the time of photographing.

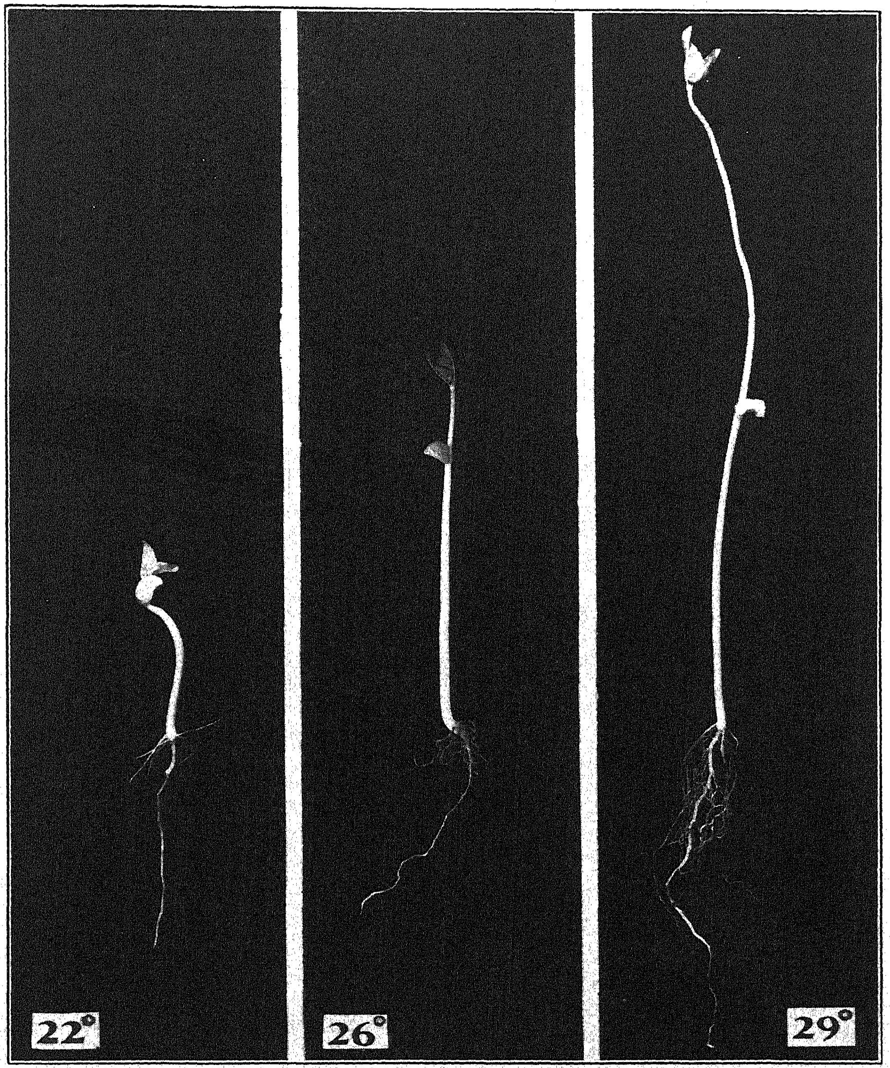

FIG. 4. Five-day-old seedlings grown in darkness at 22, 26, and 29° C.[3]

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[3] Figures 4 and 5 are published with the aid of the Lucien M. Underwood Memorial Fund.

TABLE 1

Green weights (g.) of organs of plants grown in light, some at 29° C., others at 24° C.

	29°						24°					
Age days	Cotyledons	Hypocotyls	Roots	Primary leaves	Upper stems & compound leaves (epicotyls)	Total	Cotyledons	Hypocotyls	Roots	Primary leaves	Upper stems & compound leaves (epicotyls)	Total
1	0.30	0.02			....	0.32	0.28	0.02		..	....	0.30
2	0.29	0.06	0.07	0.013	....	0.44	0.32	0.04	0.06	0.01	..	0.43
3	0.28	0.12	0.11	0.04	0.012	0.56	0.32	0.07	0.06	0.031	0.005	0.48
4	0.22	0.23	0.25	0.10	0.04	0.84	0.30	0.12	0.11	0.06	0.015	0.61
5	0.16	0.26	0.41	0.24	0.13	1.20	0.26	0.23	0.19	0.11	0.05	0.84
7	0.07	0.21	0.78	0.37	0.16	1.59	0.11	0.20	0.51	0.33	0.10	1.25
9	....	0.18	0.85	0.42	0.20	1.65	0.09	0.15	0.84	0.40	0.11	1.59
11	....	0.16	0.96	0.50	0.21	1.83	....	0.15	1.07	0.54	0.14	1.90
13	....	0.17	1.05	0.55	0.29	2.06	....	0.15	1.13	0.54	0.14	1.96
15	....	0.17	1.25	0.54	0.41	2.37	....	0.15	1.36	0.60	0.17	2.28

TABLE 2

Total ascorbic acid (mg.) in organs of plants grown in light, some at 29° C., others at 24° C.

	29°						24°					
Age days	Cotyledons	Hypocotyls	Roots	Primary leaves	Upper stems & compound leaves (epicotyls)	Total	Cotyledons	Hypocotyls	Roots	Primary leaves	Upper stems & compound leaves (epicotyls)	Total
1	0.032	0.009		0.002		0.043	0.033	0.009		0.002	....	0.044
2	0.055	0.018	0.019	0.017	0.003	0.112	0.074	0.017	0.015	0.011	0.001	0.118
3	0.066	0.028	0.027	0.054	0.005	0.180	0.080	0.029	0.020	0.033	0.003	0.165
4	0.050	0.028	0.059	0.117	0.010	0.264	0.075	0.031	0.033	0.070	0.006	0.215
5	0.010	0.014	0.073	0.230	0.014	0.341	0.069	0.030	0.043	0.140	0.014	0.296
7	0.006	0.018	0.159	0.257	0.025	0.465	0.027	0.023	0.129	0.359	0.024	0.562
9	....	0.022	0.162	0.307	0.033	0.524	0.010	0.017	0.237	0.324	0.022	0.610
11	....	0.024	0.219	0.346	0.045	0.634	....	0.020	0.282	0.420	0.020	0.742
13	....	0.024	0.250	0.326	0.061	0.661	....	0.020	0.286	0.393	0.028	0.727
15	....	0.027	0.235	0.326	0.162	0.750	....	0.023	0.285	0.422	0.030	0.760

seventh day. After the fourth day when the stored reserves are nearing exhaustion the gain is presumably chiefly a consequence of photosynthetic action in the mesophyll tissue. The chief effect of a lower temperature after the seedlings are about to emerge is a retardation in the rate of development of the mesophyll, and simultaneously in the rate of ascorbic acid synthesis. The differences in the rate of ascorbic acid accumulation are not so great as the difference in the rate of growth at the two temperatures. During the period of extensive development of mesophyll at 24° the total ascorbic acid increased until it exceeded that of the high temperature-plants. Between the thirteenth and fifteenth days the mesophyll of the first set of compound leaves developed considerably and more so at 29° than at 24°, thus causing an appreciable increase in the total content on the fifteenth day. Had the

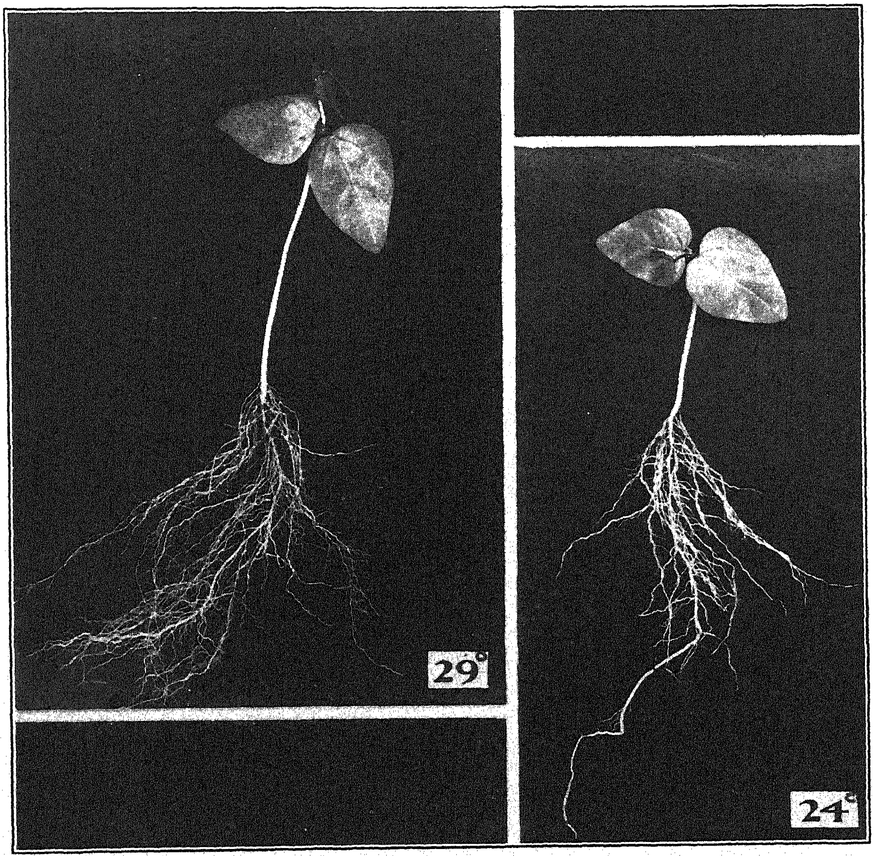

FIG. 5. Fifteen-day-old seedlings grown in daylight at 24 and 29° C.

experiment continued until the compound leaf of the 24°-plants had reached a like stage of development, the former difference in total ascorbic acid content might have again been re-established. The 24°-temperature could not be maintained after the fifteenth day, hence the experiment was terminated.

The most conspicuous difference in the appearance of the two groups of plants was the longer epicotyls and hypocotyls and finer, more flexible, and more profusely branched roots of the high temperature plants. The difference in the appearance of the plants is shown in figure 5. The roots of plants in another experiment conducted at 18–20° C. had more marked differences as compared to those of the 29°-plants than had those of the present experiment. The roots were relatively large in diameter, they were extremely brittle and not much branched. The leaves were of a distinctly paler green color than those of the high temperature-plants.

Metabolism Experiments. Most of these experiments were conducted during periods of relatively high light intensity, hence there was considerable growth response to fertilizers. Plants of approximately uniform size and appearance were employed. Green weight and ascorbic acid determinations were made in the afternoon preceding the test period. At the time the

TABLE 3

Summary of results of five tests on the metabolism of ascorbic acid in seedlings kept at different temperatures

Plants tested in p.m. previous to being kept in darkness			Plants tested in a.m. following a 12- to 18-hour period in darkness								
				Low temperature				Higher temperatures			
Time of tests	Green weight	Ascorbic acid	Time of tests	Temp. in different tests	Green weight	Ascorbic acid	Percentage change in ascorbic acid	Temp. in different tests	Green weight	Ascorbic acid	Percentage change in ascorbic acid
	g.	*mg.*			*g.*	*mg.*			*g.*	*mg.*	
5: 30 p.m. Dec. 3	15.40	5.21	5: 30 a.m. Dec. 4	13°	14.91	5.23	+0.4	24°	15.61	4.77	− 8
3: 00 p.m. Mar. 28	42.07	16.19	9: 00 a.m. Mar. 29	8°	41.44	15.68	−3.1	27°	43.22	12.62	−21
3: 00 p.m. Apr. 21	20.67	6.91	9: 00 a.m. Apr. 22	8°	22.49	7.30	+5.6	27°	23.58	5.80	−16
3: 00 p.m. Apr. 29	12.18	4.94	9: 00 a.m. Apr. 30	15°	12.72	4.80	−2.8	27°	13.43	4.18	−15
2: 00 p.m. May 6	18.09	6.15	8: 00 a.m. May 7	20°	18.50	5.87	−4.6	27°	19.05	5.19	−16

ascorbic acid assays were made, comparable cultures were placed in dark chambers kept at different temperatures. The low temperatures ranged in different tests from 8° to 20° C. and the high temperatures from 24° to 27° C. Duplicate determinations, five plants being used in each, were made of the green weights and ascorbic acid content of the different organs. In the experiments herein reported, the results were obtained with plants which received mineral nutrients.

Table 3 summarizes the results of five tests in terms of total value per plant. The results of the experiment conducted on April 29 show that there was relatively little difference in green weight (+4%) and in the ascorbic acid content (–2.8%) of plants kept for eighteen hours in darkness at 15°, whereas in those kept similarly at 27° there was a 9 per cent higher green weight and a loss of 15 per cent in total ascorbic acid.

In another experiment (March 28) in which somewhat larger and older plants were used, cultures kept for 18 hours at 8° showed no apparent gain in green weight and only a slightly lower ascorbic acid value (3.1%). Similar cultures kept at 27° appeared to gain only slightly in green weight and showed a loss of 21 per cent in total ascorbic acid. In the December 3–4 test, the plants were kept in darkness only 12 hours. The decrease in ascorbic acid in the plants kept at 27° was only about 8 per cent. The loss would probably have been somewhat greater if the plants had remained in darkness for 18 hours and also if the temperature had been kept at approximately 27° as was true in the other four tests. In all the tests the losses were found in the tops, particularly in the leaves.

DISCUSSION

The results of these tests show that the temperature of germination influences the ascorbic acid content in cowpea seedlings with respect to the total quantity present at the different stages of development, to the maximum content, and also to the final content. The temperature which favors rapid ascorbic acid accumulation is one which also favors rapid mobilization of the stored food reserves.

There is a suggestion in these results that the temperatures which are favorable to germination, if continued for a certain length of time, may be those which also permit considerable ascorbic acid accumulation. The lack of agreement between the temperature for germination and the ascorbic acid content in different types of seedlings in Moldtmann's experiments is not surprising. The types of plants which he used are known to vary with respect to the temperature which is most favorable for germination and early growth of the seedling. Relatively low germination temperatures are generally considered best for *Avena sativa* and *Pisum sativum*, slightly higher temperatures for *Zea mays* and *Phaseolus vulgaris*, and still higher temperatures for

Polygonum fagopyrum. *Vicia faba* does well over a wider range of temperatures. These variations among different types of plants with respect to the influence of temperature upon germination agree fairly well with the variations in ascorbic acid accumulation at different temperatures as reported by Moldtmann. His observation that differences in temperature had marked effects on respiratory intensity but caused no change or only a slight change on ascorbic acid content during a four hour respiratory test-period in seedlings of *Vicia faba* grown at 12°, and of *Pisum sativum* grown at 25°, differs with respect to the ascorbic acid values from the present results with cowpea seedlings, and also with his own results with *Pisum* as previously mentioned. More than a very small production of ascorbic acid with four- to seven-day-old seedlings would not be expected during a four-hour test-period. In that length of time one might expect the order of change to be no greater than the experimental error. The vitamin C values which Moldtmann obtained at 35 to 40° in the respiration tests are, however, actually lower both with *Pisum* and *Vicia* than those found at 25° and 3–5° C.

In the present tests high temperatures also favored high respiratory intensity as evidenced by greater rapidity of loss in dry weight but they also caused a definite difference in ascorbic acid content,—first, a tendency to a more rapid accumulation leading, however, to a lower maximum value and later, to a greater loss. The lower maximum value found at 29° on the fourth day suggests the possibility of previous losses, that is, that the quantity found on the fourth day does not represent the entire amount which was synthesized. It is possible, however, that the lower maximum value results from a loss in content of the vitamin precursor. Nightly losses in ascorbic acid have been shown previously (Reid 1941) to occur by the sixth night in cowpea seedlings grown under normal alternations of daylight and darkness. This is the time of exhaustion of reserves stored in the cotyledons. Similar losses presumably may have occurred during the earlier phases of growth, but were not measurable because synthesis from a stored precursor was greater than the loss.

The difference in the effects of temperature on total ascorbic acid accumulation in seedlings of cereals as reported by Kuthy (1938) and Moldtmann (1939) may possibly be caused by a difference in stage of development of the plants tested. The former investigator employed ten-day old seedlings whereas the latter disregarded age, using seedlings in an early phase of development which had attained a definite size.

Similar, though more pronounced effects of high temperatures upon the ascorbic acid content of animal tissues have been observed. Martini and Torda (1937) kept guinea pigs in chambers for an hour or two at 40–46° C. and killed them after an acceleration of pulse and respiration were noted. The ascorbic acid content of the liver and adrenals was less than half and that of the brain slightly more than half that of the controls not exposed to the heat. These investigations also found that injection of the vitamin into guinea pigs seemed to render them somewhat more resistant to the high temperature. Losses of ascorbic acid are also known to occur in the tissues of animals having fever producing-infections but it is not known definitely that the loss is a direct consequence of the increased temperature.

The results of the metabolism tests show that there tend to be losses at night at relatively high temperatures and no or only slight losses at temperatures so low as to inhibit growth and presumably respiration also. Supposedly at intermediate temperatures there would be some loss but less than at high temperatures. In the results of the May sixth experiment there is a suggestion that this is true, although tests with larger numbers of plants would be required to answer the question definitely. The results of the metabolism tests afford a possible explanation of the higher ascorbic acid content after the sixth day in the low temperature-plants grown in the light, the gain in ascorbic acid being possibly caused not so much by increased synthesis as by a slower rate of metabolic loss. It is difficult to account for the marked loss in reducing value at 20° but not at 37° C. found by Wolf (1938) in segments of detached leaves of *Bryophyllum calycinum* when kept in darkness. It would be of interest to know whether or not the respiratory rate in leaves of this type is lower at 37° than at 20°.

The effects of temperature upon the ascorbic acid content of seedlings may be said to involve relations (1) to the rate of its production from the stored food reserves, (2) to the rate of metabolic loss, and (3) to the time of emergence of the seedling above the soil. Cowpea seedlings which emerge to the light quickly, when grown under customary field conditions, can apparently tolerate a relatively high rate of loss because the early development of leaves causes them to soon become independent of stored reserves. Seedlings such as those of *Pisum* which emerge much more slowly, and especially those whose leaves develop slowly, are not favored by high temperatures during their underground phases of development. Low temperatures in *Pisum* allow synthesis of ascorbic acid and apparently tend to conserve it.

There is increasing evidence from various sources that whether or not this vitamin is of importance in relation to growth, plants do not thrive during their vegetative phase of growth except under conditions which permit an increase in their total ascorbic acid content. There is evidence also, as is here shown with cowpea plants, that in independent green plants measurable increases occur only during periods of illumination.

SUMMARY

The rates of accumulation and disappearance of ascorbic acid, as well as the respiratory intensity and rate of growth of cowpea seedlings in darkness are successively higher at temperatures of 22, 26, and 29° C.

Differences in the total ascorbic acid content of plants grown at different temperatures are associated with differences in the amount and type of growth of different organs.

It is suggested that the lower maximum vitamin C content of seedlings grown in darkness at high temperatures may be a result of a greater metabolic loss of the vitamin or, less probably, of decreased synthesis.

Within an eighteen-hour period in darkness, appreciable losses of ascorbic acid from light-grown plants occurred only under temperature conditions which were favorable to growth.

There is a lower total ascorbic acid content of the plants grown in light at 29° as compared to 24°. Reasons are advanced to suggest that it may be chiefly a consequence of a more rapid rate of metabolic loss rather than of less rapid synthesis.

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STUDIES IN THE ERICALES: A REVIEW OF THE NORTH AMERICAN GAYLUSSACIEAE; WITH REMARKS ON THE ORIGIN AND MIGRATION OF THE GROUP

W. H. CAMP

INTRODUCTION

In his Manual, Small treated the North American huckleberries as three genera different from *Gaylussacia*.[1] Shortly after, in the first of this series of Studies,[2] I questioned the advisability of these segregations primarily on the basis of our incomplete knowledge of the South American material. It has since been necessary for me to study certain species from that region in some detail. At the same time the available material of the genus was re-examined and the literature of the group brought together in greater completeness. The results of this survey are presented here.

The Gaylussacieae, a tribe of the Vacciniaceae [or if one prefers a broader phyletic interpretation, a tribe of the subfamily Vaccinioideae of the Ericaceae] is limited to the western hemisphere,[3] the greatest concentration of species being in southeastern Brazil. Since it seems apparent that the group arose in South America, where only one genus is recognized, no taxonomic segregation should be attempted until the material of that continent has first been studied, at least in some detail. So far as I can ascertain this has never been done.

The more common and widespread of the North American Gaylussacieae were, for the most part, described first as species of *Vaccinium*. We therefore find that the earliest literature dealing with them as a group was primarily concerned with their separation from this genus rather than from the South American type of *Gaylussacia*. Although *Gaylussacia* was described in 1818 on the basis of Colombian and Venezuelan material, it was not until 1841 that the North American forms now placed in the tribe were suspected as being fundamentally different from *Vaccinium*.[4] The group was then given the provisional name *Decachaena* T. & G. The same year Nuttall presented a paper in which the North American material known to him was held as separate from both *Gaylussacia* and *Vaccinium*, the emphasis being placed on its difference from the latter genus. In this paper,[5] published in 1842, he proposed the name *Decamerium* for the group. The following year Torrey[6] placed those species with which he was concerned in *Gaylussacia.* And, except for a brief and abortive nomenclatural excursion led by Kuntze[7] into *Adnaria,* they remained there until 1931. Finding that he could make some new nomenclatural combinations, Ashe[8] in that year revived the name *Decamerium* and dumped into it all the North American species which, because they were either misunderstood or unknown to him, had not been included by Nuttall. Two years later Small (*l.c.*) resurrected *Decachaena,* placed part of the North American species under it and erected two additional genera for the remainder.

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[1] Small, J. K., Manual of the Southeastern Flora, pp. 1007–1010, 1506. 1933.

[2] Camp, W. H., Bull. Torrey Club **62**: 129–132. 1935.

[3] The Bornean *Rigiolepis*, sometimes placed in the Gaylussacieae, seems to have closer affinities with the Vaccinieae.

[4] Gray, Asa. Am. Jour. Sci. **42**: 43. 1841. The same note may be found in Gray, Asa. Lond. Jour. Bot. **3**: 234. 1844.

[5] Nuttall, T. Trans. Am. Phil. Soc. II. **8**: 259–261. 1842. Although the date of this publication is generally given as 1843, there is evidence that the part containing the above cited pages appeared in December, 1842.

If we take up the problem of *Decachaena* T. & G. (1841) vs. *Decamerium* Nutt. (1842), there is little argument. The brief and informal discussion by Gray in a footnote (*l.c.* 1841), wherein he refers to it as "*Decachaena Torr. et Gray ined.,*" can scarcely be taken as a valid description, even though there is a reasonably clear outline of the diagnostic characters of the group separating it from *Vaccinium* as well as mention of the type and additional species which he intended it to contain. Ashe's note (*l.c.* p. 197) where he states that "the name [*Decachaena*] apparently was given only a subgeneric significance" is obviously incorrect, otherwise both Torrey (*l.c.*) and Gray[9] would not have listed it as a synonym of *Gaylussacia* coequal with *Decamerium* Nutt. The important fact is that Gray did not give us a formal description of *Decachaena* in 1841 and, before he could, Nuttall had already published his *Decamerium.* Its status, therefore, is only that of a nomen and should have given way to *Decamerium* in Small's treatment. However, *Decachaena* is available as a subgenus or section and, although applied too broadly, has already been used as such by Drude.[10]

THE SOUTH AMERICAN SPECIES

Before we become lost in a discussion of the less interesting but necessary nomenclatural history of the group, let us turn to the material representative of the bulk of the tribe—to the South American species.

It is not my intention to treat the South American material in anything approaching a satisfactory manner either in this place or in the immediate future. The assembling of material adequate for a definitive taxonomic treatment is impossible at the present time. The genus is poorly collected, many of the species being known only from the types or from a few scattered examples; the area wherein we find the greatest concentration of described species is in need of considerably more botanical exploration; and, because of the complicated and interlocked variabilities of the collections now before me, it is obvious that a personal knowledge of the plants in the field would be most desirable. But, even so, there is sufficient material at hand to give us a reasonably clear picture of the genic reaction-pattern of the group.

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[6] Torrey, John. Fl. N. Y. 1: 448–449. 1843.

[7] Kuntze (Rev. Gen. 1891) transferred forty-eight vacciniaceous plants—mainly of the genus *Gaylussacia*—into *Adnaria* Raf. My conclusion that *Adnaria* does not belong in the Vacciniaceae but in the Styracaceae is discussed in a paper now in press (CASTANEA) under the title "Studies in the Ericales: The Search for *Adnaria odorata* Raf., and *Arbutus obtusifolius* Raf." Since *Adnaria* Raf. (1817) properly belongs to the Styracaceae the conservation of *Gaylussacia* H.B.K. (1818) over it was unnecessary.

[The paper mentioned above has since appeared; Castanea 6: 80–83. 1941.]

[8] Ashe, W. W. Rhodora 33: 197–198. 1931.

[9] Gray, Asa. Synop. Fl. N. A. Ed. I. 1878; Ed. 2. 1886.

[10] Drude, O., *in* Engl.-Prantl, Nat. Pflfam. 4^1: 50. 1889.

Characteristically, the South American members of the Gaylussacieae are small or medium-sized shrubs, often with underground rhizomes, and with relatively small, persistent and often pubescent leaves. The majority of the species bear gland-hairs on various of the organs, a common trait of the Ericales; and the inflorescence is generally racemose, often with persistent leafy bracts.

When one examines this material, it is apparent that evolution has progressed along several lines. The leaves may have become reduced, particularly in width, often with their margins revolute, and they sometimes may be essentially glabrous. The gland-hairs have evolved into two general types: (1) clavate-stipitate structures, their filiform bases varying considerably in length, the glandular portion with no visible pellicle, and (2) capitate, subsessile glands with an obvious pellicle. There also appear to be forms transitional between these two gland types. It is also apparent that several of the lines have given rise to forms which rarely bear glands of either type except perhaps for a few scattered on the inflorescence or along the leaf margins or, on occasion, these may be lacking. In the more highly evolved forms the primitive, persistent, leafy bracts of the inflorescence may be reduced to mere bracteoles and become early-caducous. In these forms it is not unusual for the racemes also to be reduced. The flowers, although varying considerably from species to species, do not seem to show any basically different structures. It is certainly evident that the inflorescence patterns and flower structures of the South American forms do not exhibit the wide diversity found within the genus *Vaccinium* (sensu lato).

In my examination of the available South American material I have noted the presence of relatively well marked sections or species-groups, particularly toward the ends of the several lines of evolution where marked divergences in habit and structure are obvious. Yet, when the group is viewed as a whole, these lines seem to become tangled in a common plexus so that, for the present at least, I am at a loss to find any combination of characters which would serve to separate them into clearly defined or easily separable units of more than subgeneric rank. But this statement is made with certain reservations, for I have as yet made no attempt to compare the correlated leaf, gland, and inflorescence types and corolla forms, either with the known differences in anther-filament ratios (which may be merely a function of corolla length) or the differences in pubescence of the filaments; and, what is more important, I have been unable to re-examine in any completeness the carpel morphology of the various South American species. This last task will be essential in a definitive study of the group, and might serve to exclude from the tribe certain of those forms which appear to be peculiarly aberrant.

Briefly, then, with specimens of a reasonable majority of the South American Gaylussacieae before me, I am unable to discern any points of difference of sufficient magnitude which, for the present, would lead me to separate the group into segregate genera coequal with *Gaylussacia* as typified by *G. buxifolia* H.B.K. However, sectional and subsectional units may be recognized, if only for convenience in systematic treatment.

THE RELATIONSHIPS OF THE NORTH AMERICAN SPECIES

It is to be admitted without argument, if one deals solely with the North American species, that they fall into three very well marked groups. Furthermore, these groups are so distinct in their general appearance and detailed morphological characters that one readily suspects that they have had separate origins and represent different kinds—or genera—of plants. It is obvious that Small came to this conclusion while preparing his 1933 Manual. And it is to be admitted that I, too, at times in my general writings and remarks, have been swayed toward this viewpoint, being too much influenced by the "weight of authority."

Small (Man. p. 1007) left no doubt that he considered the North American material to be different from the South American for he says: "This [*Decachaena*] and the two following genera [*Lasiococcus* and *Buxella*] are often included in *Gaylussacia* which, however, technically considered, forms a group of plants confined mostly to northern South America." Small had ample precedent for keeping the North American and South American forms separate, for we find the North American material treated by previous authors as follows:

Nuttall (*l.c.* 1842)—*Decamerium.*
Hooker f.[11] (1876)—*Gaylussacia* Sect. *Decamerium;* and Sect. *Vitis-idaea* (=*Buxella* Small).
Drude (*l.c.* 1889)—*Gaylussacia* Subgen. *Decachaena;* and Subgen. *Pseudo-Idaea* (=*Buxella* Small).
Ashe (*l.c.* 1931)—*Decamerium.*

In the foregoing list, it is interesting to note that the two students of our local flora—Nuttall and Ashe—applied a single generic name to all our

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[11] Hooker f., *in* Benth. and Hook. f. Gen. Pl. 2: 573. 1876.

North American material, keeping it separate from *Gaylussacia;* whereas the systematists—Hooker and Drude—recognized two sections or subgenera, but kept these separate from the South American *Eulussacia* (Hooker as a section, Drude as a subgenus). And as further corroboration of this view that the North American and South American Gaylussacieae are separable, Sleumer,[12] in his current systema of the Vaccinioideae (as a subfamily of the Ericaceae) treats the Gaylussacieae as a tribe consisting of the single genus *Gaylussacia,* but having in it the following three divisions:

Sect. I. *Decachaena*—all North American species except one.
Sect. II. *Vitis-idaea*—the North American *G. brachycera* (Michx.) Gray.
Sect. III. *Eulussacia*—all South American species.

Thus, for a century, the continuity of the concept that the North American Gaylussacieae are phyletically separate from those of South America has been maintained.

Let us now briefly examine the North American genera as defined by Small and see in what manner—and "technically considered"—they differ from the general pattern of the South American group. We shall first consider *Lasiococcus.*

As defined by Small, the genus *Lasiococcus* consists of three species: *L. dumosus,* a species of the Coastal Plain from Louisiana to Florida and northward to Newfoundland; *L. Mosieri,* locally abundant on the Coastal Plain mainly in Florida and from there to Louisiana; and *L. orocola,* known from a single locality in North Carolina.

Small's descriptions are, with one exception, ample. He has not mentioned the type of gland-hair characteristically present on the leaf, the inflorescence, and hypanthium (or in maturity, the fruit). In this group of species the glands are clavate-stipitate and do not have an obvious secretion-pellicle.

If we now consider *L. Mosieri* and compare it with certain Brazilian species (e.g. *Gaylussacia pseudogaultheria* Cham. & Schlecht.; *G. hispidula* Meissn.) we note a great similarity. In fact, I have specimens of *Lasiococcus Mosieri* before me which I cannot easily separate from individuals of *Gaylussacia pseudogaultheria,* a species known from the States of Paraná, Minas Geraes, etc.[13] It is also obvious that these species are part of a complex related via *G. amazonica* Huber of the Amazonian low-land *campos* and *G. cacauminis* A. C. Smith of Mt. Duida (Venezuela) to *G. buxifolia* H.B.K., a Venezuelan and Colombian species, the type of the genus.

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[12] Sleumer, H. Vaccinioideen-Studien. Bot. Jahrb. (Sond.-Abdr.) 71: 375–510. 1941.

[13] The question will immediately arise as to why I do not here place *L. Mosieri* in synonymy under *G. pseudogaultheria.* I have not done so solely for the reason that the specimens of both species before me exhibit certain variations which must be considered only in the light of the type of the Brazilian form, which I do not have. The decision whether *G. pseudogaultheria* should be broadly defined so as to include *L. Mosieri,* or whether it should be rigidly delimited into two groups, so that *L. Mosieri* would include part of what is now considered to be *G. pseudogaultheria,* must wait for a definitive treatment of the group and a comparison of the types of both. It is sufficient only to point out at the present time that I am unable to separate certain forms from Florida and Brazil into different species.

It is also worth recalling that, on a recent trip to the southeastern Coastal Plain (March, 1941), I noted that *L. dumosus* had persistent leaves, at least northward into North Carolina. In Florida, *L. Mosieri* often retains its leaves in a living condition throughout the winter and well into the next season, at least until the flowers are present and the new set of leaves is well developed. Persistent leaves are, of course, characteristic of the South American members of the tribe.

So far as the general pattern of the plant is concerned *L. orocola* appears to occupy a position somewhat intermediate between *L. dumosus* and *L. Mosieri*. If the material had come from the Coastal Plain it might be thought to be only an intergrade form. However, its presence in only one place, and this an isolated, high-altitude, swampy area near Flat Rock, Henderson Co., North Carolina—in the general region of the Blue Ridge which I recognize as being rich in archetype ericaceous species—leads me to suspect that this species or its immediate ancestor may have been introduced into North America in remote times and that this single known locality represents a marked restriction of a once much wider range. It should be sought for further in similar areas in the Southern Appalachians and Inner Piedmont. Because of the accumulation of morphological reductions characteristic of the species, it is obvious that, within its group, the more northerly ranging *L. dumosus* is a derived form.

In the absence of any cytological data, no phyletic sequence will be given for these three species. It is to be noted here only that these three North American forms, segregated by Small into the genus *Lasiococcus*, are closely related and have the same plant habit, inflorescence type, stipitate glands, etc., characteristic of a group of South American species of *Gaylussacia* of which one is the type of the genus. Furthermore, if *Lasiococcus* Small (1933) could be held as separate from *Gaylussacia* the name would have been an unfortunate choice, being confusable with the previously described *Lasiococca* Hook. f. (1887), one of the minor genera of Oriental Euphorbiaceae.

Our next group for consideration is *Decachaena* (sensu Small non Gray). Here I recognize five species. These differ from the foregoing group by having capitate, subsessile glands which, at maturity, exhibit a well-marked pellicle filled with secreted resinous substances[14] as well as additional (but not constant) differences in habit, leaf form, inflorescence pattern and flower shape.

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[14] In many instances, as on mature organs under natural conditions or on herbarium material, these globules have collapsed by rupture of the pellicle, leaving the resinous ''spots'' characteristic of the group, together with the remnants of the secretion cells. In the foregoing group of species, the stipitate glands either contain the oil within the cells or secrete it on their surfaces without the formation of a notably distended pellicle. Because of their differences in viscosity, adhesiveness and drying qualities, it is my opinion that the basic compounds secreted in the two groups may be chemically dissimilar.

Of the three "sections" or species-groups previously recognized by me in the North American members of this group (Camp, *l.c.*)—in the present paper called subsections—it is to be noted that one, the *Baccatae*, has the resinous glands on both the upper and lower surfaces of the leaf, although they are much better developed on the latter. Both the *Ursinae* and *Frondosae* have these glands limited to the lower surface.

Of the five species in this series, three (*G. baccata*, *G. nana* and *G. tomentosa*) have much the same general habit, being smallish shrubs much given to the formation of extensive clones. Conversely, the remaining two (*G. frondosa* and *G. ursina*) are generally taller plants (particularly *G. frondosa*, which may sometimes reach 3 meters), neither of which form the extensive, matted clones characteristic of the previous three, although they do spread to a certain extent by means of rhizomes.

It was only natural for Gray when he described the entities *nana* and *tomentosa* to consider them merely as varieties of *G. frondosa*, a plant with which he was personally familiar. Their smaller stature would also lead one to the conclusion that they were only variants (possibly due to habitat) of the more widespread species. It is dangerous to extrapolate one's information too far, yet unpublished data available to me gives clear evidence that the archetype, diploid species of *Vaccinium* are, for the most part, low forms spreading extensively by underground rhizomes, whereas their tetraploid derivatives invariably are coarser plants and generally less given to the formation of extensive clones. As a further extension of this general principle, certain of the derived hexaploid forms may, in favorable situations, reach a height of 8 meters, often being compact monopodial shrubs.

If the Gaylussacieae follow the general pattern of the Vaccinieae (which seems quite likely) we therefore should be wary of considering the entities *nana* and *tomentosa* merely as varieties of *G. frondosa*; rather, it is more likely that the wide-ranging *G. frondosa* has been derived from one (possibly *nana*) or even by allopolyploidy from a combination of both. For this reason, and until the cytological picture of the group is known, I prefer to treat these three as distinct entities of specific rank. *G. baccata* is, incidentally, known to be a diploid species and is isolated from those forms which I suspect are diploids by differences in ecological preferences; at least its range is different.

If we turn our attention once more to the South American material, it is obvious that subsessile glands with pelliculate membranes are characteristic of another group of species (e.g. *G. octosperma* Gardn., *G. ledifolia* Mart., *G. Chamissonis* Meissn., *G. pallida* Cham., *G. thymelaeoides* Meissn., etc.),[15] apparently abundant in eastern Brazil. Regardless of the ultimate nomenclatural disposition of these forms, it is sufficient only to point out that the gland type characteristic of a group of species in North America is also found in a series of South American forms of *Gaylussacia*. In turn, a few of these do not appear to have the pellicle so well developed as in the North American species and seem, in part, to connect with additional forms indicating transition stages between this gland type and that characteristic of the more primitive—and typical—species of the genus. In habit, these South American species have much in common with the low-growing forms previously noted from North America. Of the South American species (e.g. *G. octosperma* Gardn., or at least *Glaziou 16229* from the Organ Mountains and so labeled), a few have abundant and large glands on the lower leaf surface and almost none on the upper, a condition similar to that in the subsections *Frondosae* and *Ursinae;* whereas others of them have the glands on both surfaces as in the subsection *Baccatae*.

Admittedly, the South American species here listed have smaller and, in general, more indurated leaves than those in North America with which they seem to be most closely related. But if we take these South American forms and place them at one end of a series and *G. ursina*—the coarse and thin-leafed species now limited to the Southern Appalachians—at the other end, we will immediately note that *G. baccata, G. tomentosa* and *G. nana* occupy their respective niches in intermediate positions in the plexus of forms bearing pelliculate glands here under discussion.

It is therefore obvious that the group of North American species placed by Small in *Decachaena* cannot, except on the flimsiest of characters, be held separate from South American forms which lie well within the present definition of the genus *Gaylussacia*.

We now come to the last of Small's three genera of North American huckleberries, composed of the monotypic *Buxella brachycera*. There is little to add to Wherry's excellent account[16] of the history of our knowledge of this interesting plant. Among our North American huckleberries it is certainly the best marked species on account of its heavily indurated evergreen leaves, devoid of glands on either surface. The living plant has much the aspect of certain species of *Vaccinium* and its inflorescence pattern, flower and fruit conformation serve only to heighten the illusion. In fact (and again on the basis of the North American material only) it would certainly appear to merit generic rank, the carpel morphology being the only character which gives us a clue to its relationships.

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[15] It is to be remembered that I make no warranty as to the correct application of these names, some of which may be synonyms of earlier species. They are names which are associated with important South American collections, in some instances the types, now before me and which must stand or fall only in the light of a future and much needed revision of the genus.

[16] Wherry, E. T. Bull. Torrey Club **61**: 81–84. 1934.

But in our examination of the South American material from Brazil we come upon such things as *Gaylussacia Riedelii* Meissn., and *G. salicifolia* Cham. & Schlecht., with heavily indurated and obviously evergreen leaves, their margins coarsely toothed (as are those of *Buxella brachycera*) and apparently devoid of any glands. They also have the longitudinally grooved bark (in dried material) so characteristic of *B. brachycera*. To be sure, they are coarser plants and, on occasion, may bear glands in the inflorescence, these being sometimes limited to the hypanthium. But if the Brazilian species mentioned above are not exact matches for our own plant, we have to look only to additional forms in the general region of species-concentration in eastern Brazil to find those which, on one extreme, match our plant in habit, being low, cespitose clone-formers and, again, other species completely devoid of any type of gland.

Briefly, then, had the plant for which Small erected the genus *Buxella* come from Brazil rather than from North America, it never would have been thought of as anything except a species of *Gaylussacia*. Furthermore, if Small's *Buxella* did not already have phyletic unsoundness, it certainly would have nomenclatural troubles. *Buxella* Small (1933) was already preoccupied by *Buxella* Van Tieghem (1897), a genus to which several species of Euphorbiaceae (sensu lato) from Africa and Madagascar had been referred.

CHECK LIST AND SYNOPSIS OF THE SPECIES OF GAYLUSSACIA IN NORTH AMERICA

Because of certain minor errors of citation in the literature and omissions from important bibliographic sources, as well as for the use of those preparing manuals, local notes, etc., it is thought best to list here, together with the basic and most common synonyms, the North American species of *Gaylussacia* as I understand them at the present time. The various described subspecific entities have been omitted. They will be taken up at another time following a more definitive (and it is hoped genetic) analysis of the group, together with a complete synonymy. Their inclusion in this place is thought to be unnecessary.

GAYLUSSACIA H.B.K. Nov. Gen. Sp. Pl. **3**: 275. *t. 257*. 1818.
("nom. conserv.;" see footnote 7).

(A) Plants, especially the leaf surfaces, bearing clavate-stipiate gland-hairs, their glandular portion with no visible secretion pellicle.

Section I. *Eulussacia* Hook. f.; Benth. & Hook. f. Gen. Pl. **2**: 573. 1876. (Sensu speciei typicae generis, non auctorum variorum.)

1. G. MOSIERI Small, Torreya **27**: 36. 1927. *Lasiococcus* Mosieri Small, Man. SE. Fl. 1009. 1933. *G. Mosieri* Camp, Bull. Torrey Club **62**: 132. 1935 (comb. superflua).

2. G. OROCOLA (Small) Camp, Bull. Torrey Club **62**: 132. 1935. *Lasiococcus orocola* Small, Man. SE. Fl. 1009. 1933.

3. G. DUMOSA (Andr.) A. Gray, Chlor. Bor. Am. 50. 1846. *Vaccinium dumosum* Andr. Bot. Rep. **2**: *pl. 112.* 1800. *Vaccinium hirtellum* Ait. f. Hort. Kew, Ed. 2, **2**: 357. 1811. *Lasiococcus dumosus* Small, Man. SE. Fl. 1008. 1933.

(A′) Plants, especially the leaves, bearing capitate subsessile glands with an obviously inflated pellicle.

Section II. *Decachaena* (Torr. & Gray) Sleumer, Bot. Jahrb.
(Sond.-Abdr.) **71**: 383. 1941. (Sensu speciei typicae,
non auctorum variorum. Ea est *Vaccinium*
resinosum Ait.)

(B) Leaves glandular on both surfaces.

Subsection *Baccatae.*

4. G. BACCATA (Wang.) K. Koch, Dendr. **2**: 93. 1872. *Andromeda baccata* Wang. Beitr. 111. *pl. 30, f. 69.* 1787. *Vaccinium resinosum* Ait. Hort. Kew **2**: 12. 1789. *G. resinosa* T. & G.; Torr. Fl. N. Y. **1**: 449. 1843. *Decachaena baccata* Small, Man. SE. Fl. 1008. 1933.

(B′) Leaves glandular only on the lower surface.

(C) Leaf apices acute to acuminate.

Subsection *Ursinae.*

5. G. URSINA (M. A. Curtis) T. & G.; Gray, Chlor. Bor. Am. 49, *t. 10.* 1846. *Vaccinium ursinum* M. A. Curtis, Am. Jour. Sci. **44**: 82. 1842. *Decachaena ursina* Small, Man. SE. Fl. 1008. 1933.

(C′) Leaf apices rounded to obtuse.

Subsection *Frondosae.*

6. G. TOMENTOSA (Gray) Small, Bull. Torrey Club **24**: 443. 1897. *G. frondosa* var. *tomentosa* Gray, Syn. Fl. N. A. Ed. I. **2**^{1}: 19. 1878. *Vaccinium tomentosum*, Pursh; Gray, Syn. Fl. N. A. Ed. I. **2**^{1}: 19. 1878 (as synonym). *G. tomentosa* Pursh, ex. Gray; Small, Bull. Torrey Club **24**: 443. 1897 (in synonymy, combination in error). *G. tomentosa* (Pursh) Chapm.; Small, Fl. SE. U.S. 892. 1903 (in error). *Decachaena tomentosa* Small, Man. SE. Fl. 1007. 1933. *G. tomentosa* Small; Small, Man. SE. Fl. 1007. 1933 (as synonym).

7. G. NANA (A. Gray) Small, Bull. Torrey Club **24**: 443. 1897. *G. frondosa* var. *nana* A. Gray, Syn. Fl. N. A. Ed. 2. **2**^{1}: suppl. 396. 1886. *Decachaena nana* Small, Man. SE. Fl. 1008. 1933.

8. G. FRONDOSA (L.) T. & G.; Torr. Fl. N. Y. **1**: 449. 1843. *Vaccinium frondosum* L. Sp. Pl. 351. 1753. *Decachaena frondosa* Small, Man. SE. Fl. 1007. 1933.

(A″) Plants eglandular.

Section III. *Vitis-idaea* Hook. f.; Benth. & Hook. f. Gen. Pl.
2: 573. 1876.

9. G. BRACHYCERA (Michx.) A. Gray, Chlor. Bor. Am. 54. 1846. *Vaccinium brachycerum* Michx. Fl. Bor. Am. **1**: 234. 1803. *Vaccinium buxi-*

folium Salisb. Parad. Lond. *pl. 4.* 1805. *Buxella brachycera* Small, Man. SE. Fl. 1009. 1933.

A NOTE ON THE AUTHORITY FOR THE COMBINATION: GAYLUSSACIA TOMENTOSA

It is possible that future questions may arise concerning my choice of authority for the combination *G. tomentosa.* For this reason a discussion of the situation is here included.

The first use of the epithet *tomentosa* was as a variety of *G. frondosa* by Gray in 1878. (For complete citations, the foregoing synonymy may be consulted). In the same place, Gray listed the source of his name as "*Vaccinium tomentosum*, Pursh, ined." There is no evidence that Pursh ever published a description of this entity, so we must conclude that Gray got the name either from some correspondence, or from a name appended to an herbarium sheet. In 1897, in a study of the genus *Gaylussacia* in the Southern States, Small headed the paragraph discussing this plant as *Gaylussacia tomentosa* Pursh, listing the original *Gaylussacia frondosa* var. *tomentosa* A. Gray as a synonym as well as "*Gaylussacia tomentosa* Pursh," but credited this last as being published by Gray "as synonym" in the same place as the original description of the variety. This was obviously an error on Small's part, for Gray had listed it as "*Vaccinium tomentosum,* Pursh, ined."

Apparently realizing this error, Small in his 1903 Flora assigned this combination to Chapman. This was repeated in the 1913 edition. I have searched through all of the editions and as many of the various printings of Chapman's Floras as are available, as well as his few writings outside of these, and have been unable to locate any such combination, or any mention of the name even as a variety, and am forced to the conclusion that this was a further error on Small's part.

In 1933, in his Manual, Small resurrected the invalid genus *Decachaena* and made the combination *D. tomentosa,* listing *G. tomentosa* Small as a synonym. This, I think, can be taken as clear evidence that by 1933 Small realized his *G. tomentosa* Pursh ex Gray of 1897 and his *G. tomentosa* (Pursh) Chapman of 1903 were both in error.

It is my opinion that, since Pursh never gave us a description of the plant, mention of the authority for the name by Gray in synonymy as "Pursh, ined." does not constitute valid publication and that Gray should be credited with having first published the name as a taxonomic entity. Furthermore, even if he did assign the combination *G. tomentosa* first to Pursh and later to Chapman, it was Small himself who, apparently by accident, made the combination in 1897. It is therefore my conclusion that the authority for the combination should be: *Gaylussacia tomentosa* (Gray) Small.

It is to be further noted that, although the combination *Gaylussacia tomentosa* has been in common use in American botanical literature since 1897, I find no record of it either in the Index Kewensis and its Supplements or in the "Card Index of Genera, Species and Varieties of American Plants, 1885 to date"—this last commonly called the "Gray Herbarium Cards." This omission can scarcely be blamed on the editors of these indexes, for when the combination was made it was done in such a manner as to lead those who collate these invaluable bibliographic services to the conclusion that it was one which surely must have been listed previously.

THE NORTHWARD MIGRATION OF GAYLUSSACIA

The problem of origin and dispersal. It is with a certain temerity that I discuss the broader aspects of the distribution of the genus *Gaylussacia* in this place and prior to a much needed taxonomic revision of the genus. Yet I cannot forego the opportunity of remarking upon the close affinity of certain of our North American plant-groups with those of South America, and the need to consider them before we attempt any segregations in our own. Too often, a familiar group, when examined solely in the light of knowledge based upon a restricted area, tends to lead one into the pitfall of a hasty and misguided taxonomic segregation; whereas, if the group as a whole is studied it may be seen that the apparently separable local material represents only the end-products of a series of evolutionary lines stemming out of a common plexus. The North American huckleberries certainly illustrate this point.

If one follows Sleumer's latest systema (which we trust is only tentative) and puts all the South American members of *Gaylussacia* into a single subgeneric group, it is obvious that the genus becomes (if there is such a thing) monosectional, for the remaining sections—including only the North American species—are much less variable, have close relatives there and should be placed with parallel material now in the supposedly wholly South American Section *Eulussacia*. Where the material warrants and exhibits even habital differences it is sometimes advisable to make regional divisions for the convenience of easier key construction. But to make phyletic divisions solely on a geographic basis sometimes leads to an absurdity, such as finding two forms as those going under the names *G. Mosieri* and *G. pseudogaultheria* placed in different sections, or even genera—forms between which I can scarcely discern varietal differences.

This close affinity of our North American huckleberries with those of South America needs to be considered rather carefully from the standpoint of plant migration. Of course, birds can always be used to explain apparently unusual distributions. It is true that birds do eat huckleberries, and this is probably their major method of dispersal. But it is approximately four thousand miles between the northernmost known plant of *G. pseudogaultheria* and the southernmost plant of *G. Mosieri*, its scarcely separable relative. And that, to me at least, would seem to be an unusually long non-stop flight for most of our frugivorous birds. Furthermore, even greater distances separate the other North American species from their South American relatives. Therefore, our problem is to reconstruct a picture of the paleogeography of the area bounded by the outlying members of the genus; to ascertain, if possible, where they might have had their origin and whether they migrated from that area in a normal manner by gradual steps across existing land (or at most across short distances of water), or whether we will be forced to the conclusion that some unusual type of dispersal has been operative in the dissemination of the group.

Historical backgrounds of the present distribution in South America. The genus *Gaylussacia* has three centers of concentration, the primary being in eastern Brazil, where we find about forty species. Two secondary centers are found, one in northwestern South America from northern Peru to Colombia (with minor outliers in Venezuela); the other is in eastern North America. Both of these last mentioned areas have the same number of recorded species (i.e. 9, with the exact number for South America being less certain than for North America).

I cannot here go into a lengthy discussion of old land areas and their relation to centers of plant dispersal, but the correlation between the present distribution of *Gaylussacia* and certain land masses known to have been emergent for a long time is so close that to speculate on the dispersal of the genus requires a brief consideration of these areas and the possibility of their former connection.

In the geological part of this discussion I make no pretense of any great originality, but have drawn freely from the writings of Schuchert,[17] Branner,[18] James,[19] Tate,[20] Hitchcock,[21] and others. However, not being a professional geologist or geographer, I have had no great hesitancy in making certain generalizations from which, otherwise, I might be restrained, especially where the known facts of phytogeography would seem to warrant such conclusions.

As nearly as I can ascertain there are today in South America five areas of varying size whose surface rocks give evidence of great antiquity: (1)

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[17] Schuchert, Charles. Historical Geology of the Antillean-Caribbean Region. Pp. 811. John Wiley & Sons, Inc. New York. 1935.

[18] Branner, John Casper. Bull. Geol. Soc. Am. **30**: 189–338. Map. 1919.

[19] James, Preston E. Ann. Assoc. Am. Geog. **33**: 165–193. 1933.

[20] Tate, G. H. H. Geog. Rev. **28**: 452–475. 1938.

[21] Hitchcock, C. B. (Cerro Duida and the Guayana Highlands), *in* Gleason, H. A. Bull. Torrey Club. **58**: 284–287. 1931.

Southern Chile and parts of Patagonia. (2) Portions of the mountains of eastern Brazil. (3) The Choco borderland, which probably extended from Colombia southward into Ecuador and which today has on its eastern rim the Cordillera Occidental. This borderland, which once must have extended westward into what is now the Pacific Ocean, and which has on it by far the oldest of the three northern Andean chains, may once have had connection southward with the Chilean-Patagonian mass. (4) The Santa Marta massif in northern Colombia. (5) The "Guayana Shield" having in its center the Sierra Parima and the much more publicised Sierra Pacaraima and their floristically dramatic outliers (Roraima, Duida, Auyantepui, etc.). To these areas, one ought, perhaps, add "Paria," the now nearly defunct "southern frame of the Caribbean Mediterranean," a land which, according to Schuchert, lay athwart northern South America during the Paleozoic and probably the earlier Mesozoic.

It would seem probable that, throughout the later Paleozoic and the early and middle Mesozoic, much of South America was emergent and colonizable by land plants. With the advent of the Cretaceous, the surface of South America underwent a drastic change, for large areas of it were inundated by marine transgressions. But, even so, certain upland areas remained—islands on which such land plants as were present could have been preserved during those times. As nearly as I can ascertain, these areas were: certain portions of the present mountain systems of eastern Brazil, the Chilean-Patagonian mass, the one remaining rim of the Choco borderland, and possibly the center of the Santa Marta massif. It is altogether probable that additional smaller island areas may have existed.

The Guayana Shield as now interpreted, an area stretching from the present Andes to the Atlantic and from the Orinoco southward nearly to the Amazon, is a special problem. It is the opinion of Schuchert, Tate, and Hitchcock (*l.c.*, and based in part on the work of Liddle on Roraima) that the sandstone which makes up the massive table-mountains in the central portion of the Guayana Shield was deposited during the Lower Cretaceous. It is the opinion of Hitchcock (*l.c.*, p. 285) that the peaks of the Parima Range are made up of igneous or metamorphic rock—this opinion being based on their contours as viewed from the top of Duida. It is therefore possible that the center of the Guayana Shield—the Sierra Parima—may also have been emergent during the Lower Cretaceous and an additional center of refuge for land plants in South America during that time. One thing, however, is certain. If the massive sandstone layer on much of the Guayana Shield was laid down as recently as the Lower Cretaceous (and it may be much older), the central portion of the area has been continuously emergent at least since that time and colonizable by an upland vegetation.

So far as our immediate problem—the genus *Gaylussacia*—is concerned, we have already noted that its greatest concentration of species is in eastern Brazil. Its principal center of development, therefore, is on and around one of these anciently emergent areas. The other South American center is on the rim of the equally ancient Choco borderland. After what must have been an extremely old primary dispersal, a few forms have migrated into the younger (Upper- and post-Cretaceous) Andes of Colombia and Venezuela and onto the Amazonian *campos*, one species only as yet being known from the center of the Guayana Shield, although this last area is otherwise relatively rich in ericaceous material. From its concentration in areas known to have been long emergent and its apparent scarcity on those of later age, it would seem likely that the pattern of genetic variability of *Gaylussacia* was already well defined and the genus widely dispersed in South America in Cretaceous time.

The migration across Antillia. If *Gaylussacia* were confined to South America the problem of its dispersal would not be so complex, but the genus has nine species in eastern North America. As has been previously pointed out—and contrary to traditional taxonomic practices—the North American species, instead of being morphologically remote and easily separable from those of South America, show a strong affinity with them (in one case apparently being conspecific), and in general give every evidence of being derived types. The problem, then, is to get certain of the basic forms of the genus out of South America and into North America.

I shall not here enter into controversy with paleobotanists concerning the origins of the floras on the continental masses now called North America and South America, of their relations with the floras of other continental masses, or of the whole problem of paleoclimatology in relation to early plant migrations. "Land bridges" have been invented and later destroyed by contemporary authors; and the whole question of continental displacement in relation to early plant dispersals is in need of clarification, especially when one reviews the more than casual phytogeographic connections of various land masses now widely separated. Considering only the immediate problems of dispersal within the Western Hemisphere, it is becoming evident that once there must have been a much broader land-connection between North America and South America than now exists—a connection which lay to the east of the present narrow "Isthmian Bridge." The sometimes striking phytogeographic affinities between eastern (Atlantic) North America, across the Caribbean and into northeastern and eastern (Atlantic) South America are certainly suggestive of this viewpoint. There is, of course, ample evidence for a series of migrations between the Pacific sides of the two continents.

It would appear that the great bulk of the intercontinental migration was from the south toward the north.[22] Exceptions are known, but those which I have examined have almost invariably involved the more highly developed and recently evolved members of their group; and, further, these recently arisen members seem, for the most part, to have used the connection on the Pacific side and not spread into South America from North America by an eastward route. Therefore, relying on such phytogeographic and geological evidence as I can gather, I must come to two fundamental conclusions: (1) that a broad land-connection, portions of it probably with considerable altitude, existed for at least part of the Cretaceous between the Atlantic sides of North America and South America, in addition to the generally assumed connection on the Pacific side; (2) that this connection, although broken in the Eocene, was partially reformed at some time during the Oligocene. It is not necessary to assume that, in Oligocene time, the land was completely continuous but, at least for a while, a segment of northern South America must have been connected with an emergent portion of Antillia and this, in turn (perhaps at a later date), with the (then) large offshore island which since has become Florida. The nucleus of this repeatedly expanded and contracted "island" certainly has not been under water since the Eocene and today holds a rich flora derived from the south (being the center, among others, of the distribution of the North American segment of the *Gaylussacia Mosieri-pseudogaultheria* complex). This Florida "island" was connected with the North American mainland during the Miocene.

Returning to our consideration of *Gaylussacia*, it becomes apparent that the genus arose in South America for there, today, we find it as a series of interlocked species-groups still differentiating out of a common plexus, only three of which have given representative members to North America. Nor is it necessary to assume that the early representatives of these groups migrated northward at the same time. Plants very like our modern submontane forms, *G. ursina* and *G. brachycera*, surely must have been in the vanguard of this movement. Here, too, I should like to place the prototype of the wide-ranging *G. baccata* with its upland and lowland forms. *G. tomentosa* and *G. nana*, being somewhat more closely related in habit to species now present in South America, may have arrived later but, even so, they seem to be strongly tinctured with the characters of *G. ursina* and may represent segregate and now nearly homogeneous races following the complete obliteration of a lowland phase of *G. ursina* by several essentially different South American forms.[23] *G. frondosa* gives all evidence of having arisen in North America out of species already present.

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[22] Any student of the Caribbean floras will immediately recognize that here I am not giving adequate consideration to that region. One of the remarkable things in the Caribbean is its west-east set of phytogeographic connections extending from Central America across the area in such a manner as to make it appear that we are looking at the isolated relics of the floras of an ancient continental mass traversed by a series of nearly parallel mountain ranges. Complicating this picture is the series of well marked south-north lines of connection. The old block of Antillia has been ground between the shifting continental masses of North America and South America; it has been segmented, and the blocks sometimes laterally displaced for many miles; it has been warped and buckled, great folds having been thrown across it in several directions; and it is the directions of the displacements and the trend of these folds and upthrusts—when they were above the waters of those ancient seas—which, to a large extent determined the present complicated floristic pattern of the Caribbean. I am in this place dealing only with a group which apparently crossed from South America *into* North America.

There remains for our consideration only *G. Mosieri* and its close relatives. Whether *G. orocola* of the Blue Ridge represents an early introduction into North America and is the form from which *G. dumosa* has been derived, with *G. Mosieri* being a more recent introduction, or whether they all have been derived from the same immediate source, is in the realm of pure speculation and must await further cytological analysis. They are so closely related that I find it difficult to think otherwise than that they have arisen in North America from a common ancestor, in appearance much like the present *G. Mosieri.* Yet, an examination of these and closely related South American forms leads me to the conclusion that *G. orocola* and *G. dumosa* are more nearly related than *G. orocola* and *G. Mosieri;* that the *G. orocola-dumosa* unit came to North America prior to the advent of *G. Mosieri,* but that both of these (the *G. orocola-dumosa* unit and the *G. Mosieri-pseudogaultheria* unit) have been derived from the same South American prototype.

Without correlative data we should be forced to disavow normal peristaltic activity in the avian alimentary tract and call upon our feathered friends for help in some peculiar manner to explain the dispersal of this group of plants over more than short distances. There is, however, another line of evidence which we shall briefly pursue: we shall consider not one species or even a single genus, but a phyletic-ecological consociation. A species of *Gaylussacia* (*G. amazonica* Huber), closely related to the *G. pseudogaultheria-Mosieri* unit and its nearest relatives, is found on the *campos* of the Amazon Basin, a region of comparatively recent origin and historically related to the outer Coastal Plain of North America where various of our own species of this genus are so well developed (at least the regions are both of Late Tertiary and Quaternary age).

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[23] I see nothing phyletically improbable in such a viewpoint. It has been accomplished repeatedly in *Vaccinium*, where I have had opportunity to analyze the situation in greater detail against a background of experimental data. In this genus certain species with excellent and ''natural'' ranges are obviously the result of the blending of heredities of portions of two or more well-marked basic species. In certain instances these ''species'' (e.g. *V. corymbosum*) have been reproduced by controlled breeding. Furthermore, their characters, consisting of a series of multiple allelemorphs, do not segregate as would be expected of simple unit factors, but enter into combinations forming blended populations in areas of isolation which react much as those of essentially homozygous species. Such, therefore, may easily have been the history of both *G. nana* and *G. tomentosa.*

If we consider even a brief list of the more common plants on these *campos* we will see the close phytogeographic connection between the two areas.[24] To be sure, a group of purely tropical things is present there. But if a student of the flora of the Coastal Plain of eastern and southeastern North America—and one who knows only this flora—were to venture onto those sunny and acid-soil Amazonian savannas he would find many species very similar to those with which he is familiar: examples of *Schizaea*, of Xyridaceae and Eriocaulaceae, *Burmannia*, Melastomaceae, Gentianaceae, various common Gramineae and Cyperaceae, *Cuphea*, *Ilex*, *Brysonima* and *Leucothoë*, to mention only some of those which are more common and which are not widespread "weed-species." Many others could be included.

Perhaps the greatest stumbling block to a complete understanding of the direct south-north migration of *Gaylussacia* is the fact that it is not today known from the interior of the Caribbean area—the region of old Antillia. But its apparent absence is no proof that the genus did not migrate from South America into North America by that route and by gradual steps, without the aid of any spectacular non-stop avian transportations. The exact sequence of geological events throughout the Caribbean is still much in question and one needs only refer to the work of Hess on the basic island arc structure in the West Indies[25] to sense the variant opinions and the need for a reinterpretation of the geohistory of this region. This is particularly true of those areas which, periodically or locally for long periods, have been out of water and colonizable by plants, rather than those which have been so often inundated. It is obvious that whole segments of Antillia have been lost, some of these apparently rather late in the Tertiary; segments which, if they were above water today, might serve to clarify what, to us, seems to be a rather complicated and insoluble sequence of plant migrations, often not at all correlated with the present series of "island stepping stones" which swing the arc of the Caribbean (see again footnote 22).

I have little hope that *Gaylussacia* will yet be found even in the poorly explored and geologically ancient mountainous parts of Oriente in Cuba or on the pre-Tertiary Cordillere Centrale of Hispaniola, but the possibility should not be excluded. Such a discovery would certainly be welcome news to an ericologist. However, it is more likely that such members of *Gaylussacia* as might have been on Antillia during the Tertiary were, like most of their congeners, poorly adapted to compete under tropical forest conditions and must have existed only in sunny, acid savannas, or at most associated with open forest stands, even as today.

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[24] Ducke, Adolph. A Amazonia Brasileira. Anais Prim. Reun. Sul-Amer. Bot. **1**: 275–287. 1938. For a discussion of these Amazonian *campos* and the related and widespread non-forested areas to the southeast, the center of *Gaylussacia*-concentration in Brazil, see: de Sampio, A. J. Phytogeographia do Brasil. Bol. Mus. Nacional (Rio de Janeiro) **6**: 271–299. 1930; especially the map opp. p. 296.

[25] Hess, H. H. Proc. Am. Phil. Soc. **79**: 71–96. 1938.

If I am interpreting the available evidence correctly it would appear that the Oligocene was the last chance for the *Gaylussacia*-population of South America to place members within easy striking distance of North America by natural means of dispersal and, if we *must* call in the birds, without forcing them to fly unreasonable distances over water. This is brought out particularly well by one of Schuchert's maps (*l.c.,* Plate 11). I would, for the present, want to make only one important change in this chart. It is my opinion that, during the Lower Oligocene at least, the eastern part of Antillia was connected with parts of northern South America by a broad band of open, mixed lowland-savanna country; a type of terrain which must have extended northward in broad arcs to the margin of present-day Florida, being then separated from the Florida "island" by only a narrow strait, probably less than 100 miles wide, and easily crossed by birds. Or it is possible that these areas may even have had actual surface communication for a time and that more recent geological events have obscured the record.

The Miocene witnessed the extreme deformation and almost complete submergence of the bulk of Antillia, leaving emergent only a few small and widely separated islands. There was a brief recovery during the Lower Pliocene, but the Pleistocene again brought on a rather general inundation; this being followed by a recent partial uplift.

Had such members of *Gaylussacia* as were on central and eastern Antillia in the Oligocene been so placed that they could migrate into these small residual island centers of refuge during the Miocene and Pleistocene submergences, it is unlikely that they could have competed with the forest vegetation already there. Of it they could have, the recovery (as in Cuba) of available and ecologically suitable habitats at the end of the Pleistocene would have been most difficult, for large areas were now highly charged with marine calcareous salts, always fatal to a group—such as *Gaylussacia*—which requires acid-soil conditions.

Briefly then, beginning in the Late Tertiary, the history of Antillia was such that it practically excluded any possibility of *Gaylussacia* having remained there; whereas conditions during part of the Cretaceous and again during the Oligocene would seem to have been ideal for trans-Antillian plant migrations.

We can, I think, exclude any possibility of the genus having come into North America by way of Central America and Mexico, in part the western segment of Antillia. There are today in those regions too many groups of the Ericales having a strong relationship (even conspecific) with those of eastern North America and which (in the latter) have the same ecological requirements as *Gaylussacia.* Had the genus come by that route in sufficient numbers so as to have given the morphologically different and ecologically distinct forms which now exist in North America, some would surely have been preserved along with their ericalean relatives. But none are known.

Conclusions on the migrations into North America. It is on the foregoing set of collateral evidences that I base my first conclusion that there probably were two major cycles of immigration of the genus *Gaylussacia* into North America. Although having today an obvious phyletic connection with forms now existing in South America, the upland and apparently earliest of these immigrants seem to have had sufficient time to evolve into species quite distinct from their nearest relatives. The more recent introductions into North America appear to have been mainly lowland forms and show no such marked differences being, in part, apparently conspecific with South American material. It is also concluded that the propagules of the ancestral forms giving rise to the present species were not carried directly from South America into North America, but that the dispersal was of a type normal to the group—one by gradual migration on land then existent, or at most for only short distances across water. Lastly, it is concluded that the migration was across the eastern portion of Antillia and not by the present "Isthmian Bridge."

SUMMARY

An examination of the Gaylussacieae, a tribe of the Vacciniaceae, reveals that, as a group, it has undergone its major evolution in South America. There, definite lines of phyletic divergence are evident, but it is obvious that they have been derived out of a common plexus, forms being present today which bridge the gap between the more primitive members of these groups. As a consequence, it would seem prudent not to attempt any generic segregation within the South American representatives; that they all be considered as part of the genus *Gaylussacia*.

It has been traditional for the past century to consider the North American Gaylussacieae as being in some way easily separable from the South American forms, for they have been treated by various authors as separate sections of a genus, as subgenera, or even different genera. Considered alone, the North American material consists of three well-marked groups, but when critically examined each of these gives clear indication that it has been rather directly derived from South American material, having counterparts in the common plexus of the genus. In one instance there is even an apparent specific link between the two continents. If the South American material is to be maintained as a single genus, it is therefore obvious that the North American forms must be included. It is certainly clear that any separation into subgeneric categories on a geographic basis violates the fundamental phylogeny of the group.

It is evident that the genus *Gaylussacia* has undergone its major development on the ancient uplands of southeastern Brazil; that some of its lines of descent are also represented in northern and northwestern South America; and that derived but closely related forms are present in North America. From this evidence we must conclude that the genus migrated into North America from South America.

It seems apparent that there were two major introductions of the genus *Gaylussacia* into North America; one, primarily of upland forms, during the Cretaceous and another, of lowland forms, during probably the Oligocene.

Since there is no evidence that the genus entered North America by way of the present "Isthmian Bridge," or even in the same region by a much earlier connection, it is concluded that the northward migration of *Gaylussacia* must have taken place across the eastern segment of Antillia. This opinion is further substantiated, not only by certain present close relationships within the genus but also by residual, but strong, phytogeographic connections in other groups between parts of eastern South America and eastern North America. The absence of the genus today from the interior of the Caribbean area is no proof that the group did not move northward by that route, for the Late Tertiary and Recent history of the area involved a series of events resulting in the formation of habitats ecologically unsuited to its survival there.

Gaylussacia, an obviously ancient genus is, therefore, another of those genetic complexes giving clear indication of the derived nature of the North American floras. It is another link in the ever strengthening chain of evidence that many angiospermous groups underwent their primary evolution in the Southern Hemisphere and subsequently migrated into the Northern Hemisphere.

THE NEW YORK BOTANICAL GARDEN
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SUPPLEMENTARY NOTES ON AMERICAN LABIATAE—II[1]

CARL EPLING

TEUCRIUM

T. BICOLOR Sm. CHILE—COQUIMBO: Depto. Ovalle, Cuesta de Cavilolin, *Worth and Morrison 16453.* Depto. Illapel, Quebrada Luncuman, *Worth and Morrison 16502.* SANTIAGO: Depto. Melipilla, La Viscachas, associated with *Schizanthus, Phacelia* and *Alstroemeria spathulata.* The flower color of this species, as with the following, may vary from pure white or cream-color to maroon, at least on the lower lip. Both extremes grow together.

T. NUDICAULE Hook. CHILE—ATACAMA: Depto. Huasco, near Huasco, *Worth and Morrison 16428.* "Flower cream-colored; lip white-pubescent, velvety maroon inside. Two collections of apparently this same genus at Taltal (viz. *Worth and Morrison 15832; Beetle 26177*) but none with this color lip. Some here lacked it" (collectors' note). Depto. Elqui, 20 km. al sur de Vicuña, *Wagenknecht 4237.*

T. LAEVIGATUM Vahl. ARGENTINA—BUENOS AIRES: 77 km. southeast of La Plata near mouth of Rio de la Plata, *Eyerdam and Beetle 23275.*

STACHYS

S. LINDENII Benth. GUATEMALA—SAN MARCOS: Volcan Tacana, 2500–3000 m., *Steyermark 36264.* SUCHITEPEQUEZ: Volcan Zunil, 500–800 m., *Steyermark 35439.*

S. ERIANTHA Benth. MEXICO—VERA CRUZ: Los Pescados, 10,500 ft., *Balls 4607;* Apitza, Ixtaccihuatl, 12,600 ft., *Balls 5137.*

S. (?) GLOBOSA Epling. MEXICO—VERA CRUZ: Loma Grande, Mt. Orizaba, 9,200 ft., *Balls 4353.* Assuredly a member of the species group to which *S. globosa* is assigned, characterized by the relatively short upper lip and scarcely exserted stamens. However, although the pubescence is very like that of *S. globosa,* the flowers are larger and the calyx teeth less pronouncedly spinose.

S. TRUNCATA Kunze. CHILE—ANTOFAGASTA: Depto. Taltal, 6 km. east of Taltal, *Worth and Morrison 16117.* Assuredly this species, previously known no further north than Coquimbo, and with a slight but unmistakable annulus in the corolla tube.

S. BORAGINOIDES C. & S. MEXICO—MICHOACAN: Mt. Tancitaro, near Uruapan, 2075 m., *Hinton 15501.* Apparently referable to this species, previously known only from Vera Cruz and Hidalgo.

S. APERTA Epling. This species is known only from a single specimen collected by *Macbride* near Muna (*no. 3963*). The present specimen, collected by *Worth and Morrison* (*no. 15661*) in PERU, Depto. AREQUIPA, Prov. Camana near Atiquipa, corresponds fairly well, save in the degree of exsertion of the stamens. In the type, they are exserted 3 mm.; in this specimen, about 1.5 mm. To this specimen may also be added one collected by *Killip*

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[1] See Bull. Torrey Club **67:** 509–534. 1940.

and Smith (*no. 22253*) in Depto. AYACUCHO at Pampalca, between Huanta and Rio Apurimac and one collected in Arequipa near Chala by *Weberbauer* (*no. 7191*). Whether these are conspecific remains to be determined by more collections. Suffice it to say that they are the only known Peruvian *Stachys* of this habit, with corolla tubes 6–8 mm. long, which have a well-defined annulus. They are apparently the Peruvian representatives of a complex group which ranges from Chile (*S. Macraei*) to California (*S. bullata*).

SCUTELLARIA

S. (?) HOOKERI Epling. COLOMBIA—Comisaria del CAQUETÁ, Cord. Oriental, Quebrada del Rio Hacha, Cajon de Pulido, 1700 m., *Cuatrecasas 8747* (Herb. Nac. Colomb.). This species was described from cultivated plants, grown from Peruvian seeds. *Poeppig 1535,* collected near Pampanacio, Peru, is seemingly identical with the type. The present specimen is identical in pubescence with Poeppig's plant, pubescence unique in the South American species of *Scutellaria,* and is very similar in habit. The leaves of Poeppig's plant are pale and seemingly whitish beneath, whereas those of the present specimen are purple beneath.

S. BENTHAMIANA (Mansf.) Epling. PERU—APURIMAC: Prov. Abancay, slopes of Orckone Grande, Trancapata, near Curasuasi, 3100 m., *Vargas 9622.* Said by the collector to have been collected by him also in Paruco, Cuzco.

HEDEOMA

H. FLORIBUNDUM Standley. MEXICO—SONORA: Sierra des Pappas, *Gentry 631.*

MINTHOSTACHYS

M. MOLLIS Griseb. PERU—LA LIBERTAD: Prov. Santiago de Chuco, north of Cachicadan, *Stork and Horton 9957.*

SATUREJA

S. TAXIFOLIA (Kunth) Briq. ECUADOR: Cuenca, Quebrada de Chushkin 8,500 ft., *Balls 7079.*

S. ACUTIFOLIA (Benth.) Briq. PERU—CAJAMARCA: Prov. Cutervo, Sucse R. Valley west of Socota, 2800 m., *Stork and Horton 10097.* Known previously only from the original collections of Mathews at Chachapoyas. Those specimens are notably silky with appressed hairs on the upper leaf surface and twigs. The present specimens are hardly silky in pubescence, but have the same habit and essentially the same flowers. The calyx teeth, however, are as much as 4 mm. long.

S. Panicera Epling, sp. nov. (Gardoquia). Frutex altitudine ad 1.5 m. ramulis pilis brevibus subappressis hirtellis; foliorum laminis crassiusculis obtusis modo rhomboideis et in basi cuneatis modo deltoideo-ovatis et in basi truncato-subcordatis, 1–2.5 cm. diametro, marginibus serrato-crenatis, revolutis, pagina superiore rugosa glabra viride, inferiore dense albo-tomentosa; petiolis 2–5 mm. longis; floribus circiter 6 in cymulis breviter pedunculatis axillaribus, bracteolis linearibus 3–4 mm. longis subtentis; calycibus costatis extus pilis brevibus crispule hirtellis, tubo circiter 6 mm. longo et dentibus deltoideo-lanceolatis acutis, inferioribus 3.5–4 mm. longis, superioribus similibus in basi connatis; corollarum auriantiacarum tubo 20–25 mm. longo, labia superiore 4–5 mm. alta.

PERU—LA LIBERTAD: Prov. Santiago de Chuco, Cachicadan, 2800 m., *Stork and Horton 9956* (TYPE, Univ. Calif., L. A.).

In habit this proposed species is scarcely different from *S. rugosa* (R. & P.) Briq. and very similar to *S. tomentosa* (Kunth) Briq. The first named is known only from the type, the locality of collection of which is not known, save that it is ascribed to Peru. The second named is an Ecuadoran species, frequently collected. It is known from Peru from a single collection made near Huanta by *McBride and Featherstone* (*no. 2084*); it is not certain, however, that this specimen is conspecific with the plants of Ecuador. The flowers are similar. The present specimen differs from both *S. rugosa* and *S. tomentosa* primarily in the flowers. The calyces of *S. rugosa* are about 7 mm. long, with a fine spreading pubescence, the teeth being about 2.5 mm. long. The corollas are notably shorter, the tube being only about 1 cm. long. While it is true that the corollas of *S. tomentosa* are about the same as those of the present plant, the calyx teeth appear to be uniformly shorter, rarely over 2.5 mm. long. Much more material is needed satisfactorily to dispose of this complex.

According to the collector's note the species is gathered in the locality cited and sent to Trujillo for sale in the market as a medicinal herb. It is known as "Panicera."

ASTEROHYPTIS

A. SEEMANNII (Gray) Epling. MEXICO—DURANGO: Tamazula, *Gentry 5224.*

HYPTIS

H. (?) SIDAEFOLIA (L'Hérit.) Briq. Inadequate collections of what are probably this species have been collected in PERU—ANCASH: Prov. Santa, Lomas de la Chay, 40 km. north of Barranca, *Stork, Horton and Vargas 9203.* AREQUIPA: Prov. Camana, 10 km. east of Chala, *Worth and Morrison 15618.*

H. INVOLUCRATA Benth. MEXICO: Temascaltepec, Penon, 1700 m., *Hinton 2146;* Temascaltepec, Tejupilco, *Hinton 1597.* Previously known only from Bentham's type, collected at Saltepec by *Karwinski.* Both specimens, like the type, have the leaves and capitula in threes. The involucre is very conspicuous.

H. HIRSUTA Kunth. A specimen which is apparently referable to *H. hirsuta* Kunth, has been collected in Los Llanos, Rio Meta, near Matabubosa by *Cuatrecasas* (*no. 4242*). If this species, it is the first time it has been found in Colombia, although known from Venezuela. However, the columella of the gynobase, which in *H. hirsuta* equals the ovules in length, is seemingly wanting in this specimen. The nutlets are alveolate, however, a characteristic of the section *Xylodontes* to which *H. hirsuta* is assigned.

H. villicaulis Epling, sp. nov. (*Polydesmia: Vulgares*). Herbae perennes utrimque pilis longioribus molliter pilosae; foliorum laminis sat amplis, 8–11 cm. longis, late rhomboideo-ovatis, 6–9 cm. latis, in apice leniter acuminatis, in basi plus minusve cuneatis, marginibus dupliciter serratis, paginis ambabus molliter pilosis; petiolis plus minusve marginatis, 1–3 cm.

longis; verticillastris in spicis compactis, pedunculis circiter 2 mm. longis elatis; bracteis paucis, vix membranaceis, circiter 5 mm. longis acuminatis mucronatis, ciliatis et paulo villosis, calycibus florentibus circiter 3 mm. longis, dentibus tubum subaequantibus, setaceis, vix tamen rigidis, equilongis, tubis maturis 5 mm. longis, tenuibus, dentibus fere 2 mm. longis; corollarum tubis 5 mm. longis; nuculis oblongis in apice rotundatis.

BRAZIL—MATTO GROSSO: Maribondo, Rio S. Lourenco, IV. 1911, *Hochne 2866* (TYPE, Univ. Calif., L. A.).

H. brachypoda Epling, sp. nov. (*Cephalohyptis: Marrubiastrae*). Herbae versimiliter perennes caulibus utrimque pilis ascendenti-appressis molliter hirsutis, internodiis superioribus quam folia fere duplo longioribus; foliorum laminis subcoriaceis, ovatis, 6–7 cm. longis, circiter 3 cm. latis, in basi rotundato-angustatis, supra medium acuminatis, marginibus sat convexis, regulariter serratis, pagina superiore sparse appresso-hirsuta, tamen sublucida, inferiore pallidiore praesertim ad venas appresso-hirsuta plus minusve sericea; petiolis latioribus subnullis 5–8 mm. longis; capitulis maturis globosis circiter 1.5 cm. diametro, in foliorum superiorum vix deminutorum axillis pedunculis hirsutis 3–3.5 cm. longis elatis; bracteis lanceolatis 7–9 mm. longis, mox reflexis, hirtellis; calycibus florentibus 4 mm. longis, dentibus deltoideo-subulatis fere 2.5 mm. longis, fere glabris, tubo in maturitate 4 mm. longo, glabro; corollarum tubo 3.5 mm. longo; nuculis obscure asperulis ut videtur laevibus.

COLOMBIA—ANTIOQUIA: Cocorua, VIII. 1938, *Bro. Daniel 1530* (USNH, type). In habit this plant suggests *H. brachiata* (*Xylodontes*), also Colombian. However, the structure of the gynobase and the obscurely roughened rather than alveolate nutlets, relate it to *Cephalohyptis.*

H. pseudolantana Epling, sp. nov. (*Rhytidea*). Frutex vel suffrutex altitudine circiter 1 m., superne sat sarmentosus, nullomodo virgatus, ramulis pilis crassiusculis in basi plus minusve pustulatis ascendentibus scabropubescentibus et superne glanduloso-puberuliis; internodiis foliorum laminas subaequantibus; foliorum laminis ovatis, vix membranaceis, 1.5–2.5 cm. longis, in apice sat acutis, in basi rotundatis, paginis ambabus scabro-hirsutis, marginibus leniter et irregulariter serratis; petiolis 1–2 mm. longis; cymulis axillaribus pedunculis 3–5 mm. longis elatis; calycibus florentibus 4.5–5 mm. longis, extus dense glanduloso-puberulis et sparse ciliatis, intus supra medium piloso-annulatis tubis dentes subaequantibus sat tenuibus, dentibus deltoideo-lanceolatis, acutis; calycibus maturis etiam nuculis non visis; corallarum tubis 5.5–6.5 mm. longis.

The habit, not unusual for *Hyptis,* strongly suggests some species of *Lantana,* such for example, as *L. montevidensis.* The structure of the calyx, with its median annulus, suggests its association with *H. rhytidea.*

MEXICO—GUERRERO: Aguazarca Filo, distr. Mina, *Hinton 11266* (TYPE, Univ. Calif., L. A.).

H. pseudosinuata Epling, sp. nov. (*Cephalohyptis: Marrubiastrae*). Herbae verisimiliter perennes caulibus superne tenuiter villosis, internodiis quam folia longioribus; foliorum laminis ovatis, 4.5–5 cm. longis, 2.5–3 cm. latis (et grandioribus in partibus inferioribus ?), obtusiusculis, in basi rotundatis et ad petiolos 5–15 mm. longos plus minusve cuneatis, marginibus regulariter serratis, paginis ambabus fere glabris, tenuiter villosis; capitulis

maturis subglobosis, 18–22 mm. diametro, viridibus, in foliorum supremorum gradatim deminutorum axillis pedunculis 10–12 mm. longis dispositis; bracteis villosis, anguste ovatis, 5–6 mm. longis, in maturitate occultis; calycibus florentibus fere glabris, circiter 3.5 mm. longis, dentibus circiter 1.5 mm. longis, anguste deltoideis, acutis, subaequalibus, tubo in maturitate 3.5 mm. longo; corollarum tubo 3.5 mm. longo.

COLOMBIA—HUILA: Cordillera Oriental, bosques mas arriba de Guadalupe en Resina, 1850–1900 m., 20.III.1940, *Arbolaez and Cuatrecasas 8363* (USNH, TYPE).

SALVIA[2]

Key to Sections (p. 7, line 36). Read for "Invaginatas" "Hoehneana et."

5. S. SETOSA Fern. MEXICO—DURANGO: Tamazula, *Gentry 5243.* Apparently this, but the corolla tubes 4 mm. long and the lips proportionately longer, but still hardly equal to those of *S. monantha.*

41. S. LAVANDULOIDES Kunth. MEXICO—DURANGO: Sierra Tres Picos, *Gentry 5332.* SONORA: La Mesa Colorado, *Gentry 546.* SINALOA: Cerro de la Sandia near Panuco, *Pennell 20106.* Previously known no further north than Jalisco. These specimens seem fairly typical and are comparable to Guatemalan specimens, as for example, *Standley 58580.* The Sonoran specimen is more glabrate, but scarcely to be distinguished from *Hinton 134*, from Temascaltepec. GUATEMALA—ZACAPA: Sierra de las Minas, 1000–1500 m., *Steyermark 29701.* SAN MARCOS: Sibinal, 2500 m., *Steyermark 36070.* JALAPA: Cerro Alcoba, near Jalapa, 1300–1700 m., *Steyermark 32604;* between Quisiltepeque and Potrero Carrillo, 1800 m., *Steyermark 33020;* same place, *Steyermark 33021* (an albino).

47. S. ALAMOSANA Rose. MEXICO—SINALOA: Cerro Colorado, *Gentry 5210.* SONORA: Saucito canyon, distr. Alamos, *Gentry 688.* The second specimen, from the type locality, has sparse spreading glandular hairs in the inflorescence instead of the usual downwardly curled ones.

50. S. INCONSPICUA Benth. MEXICO—MICHOACAN: Sierra Torricillas, Coalcoman, 2420 m., *Hinton 12402; 12361.* GUERRERO: Toro Muerto, Mina, 2350 m., *Hinton 14763;* Teotepec, distr. Mina, 2500 m., *Hinton 14806.*

52. S. CHALAROTHYRSA Fern. MEXICO—MICHOACAN: Coalcoman, 1200 m., *Hinton 12329;* Coalcoman, Salitre, 1200 m., *Hinton 12171.* Known previously only from the type, collected in Jalisco.

54. S. PAVONII Benth. PERU—JUNIN: Prov. Tarma, between Palca and Carpapata, 2900 m., *Stork 10956.* Previously known only from the type, collected in Peru without data by (?) Dombey. The leaves of this specimen are somewhat more lax than the type, now at the University of Oxford, otherwise it is very similar. The sessile glands which cover the leaves and branches are evidently quite conspicuous and are said by Stork to be cinnabar red. The corollas are lemon yellow. What appears to be the same species was collected, supposedly by *Lobb* (*no. 82*), and attributed to Colombia by Hooker.

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[2] The serial numbers and cited paginations refer to a previous paper, "Revision of Salvia: Calosphace" in Rep. Spec. Nov., Beih. 110. 1939.

57. S. CORRUGATA Vahl. PERU—HUANCAVELICA: Prov. Tayacaja, Quebrada south of Salcabamba, 3300 m., *Stork and Horton 10297*. The flowering calyces are 9 mm. long and the corolla tubes are 18 mm. long, the upper lip being 10 mm. long.

58a. **S. pseudorosmarinus** Epling, sp. nov. (*Corrugatae*). Suffrutex altitudine ad 60 cm. ramis virgatis viscidis pilis minutis extensis glandulosis et majoribus crispis eglandulosis vestitis superne villosis, utrimque ad basim ramulis brevibus foliis fastigiatis ornatis submoniliformibus; foliorum laminis bullulatis habitus *Rosmarini* linearibus 1–2.5 cm. longis, valde revolutis, in apice obtusis, in basi modo truncatis modo hastatis, pagina superiore minute glandulosa inferiore obumbrata villosa; petiolis 1–3 mm. longis; floribus ut videtur solitariis in foliorum supremorum paulo deminutorum axillis positis; calycibus florentibus 9–10 mm. longis, extus viscido-villosis, trimucronatis; corollarum atro-cyanearum tubo 15 mm. longo, labia superiore 5 mm. alta, inferiore fere duplo longiore.

PERU—LA LIBERTAD: Prov. Santiago de Chuco, Cachicadan. Open shrubby hillside, clay soil, 2900 m., 25.XI.1938, *Stork and Horton 9968* (TYPE, Univ. Calif., L. A.).

This species bears all the earmarks of the section *Corrugatae* save for the fact that the flowers are borne in the axils of the upper but little modified leaves. It would accordingly be sought under *Tomentellae* in the Key to the Sections (p. 9). The Key should therefore be emended to read (p. 9, line 28) as follows:

"HH. Frutices sarmentosi vel suffrutices pilis frequenter ramosis; styli ramus anticus sat attentuatus vix complanato-deltoideus. I. Corollarum tubi ad basim valde invaginati; folia habitus *Rosmarini* 11. *Corrugatae*. II. Corollarum tubi sat ventricosi, vix tamen invaginati nisi rugis binis obliquo intus obscure ornati 3. *Tomentellae*. DD. Staminum gubernacula vel integra, etc., etc."

The foliage and the dwarf lateral branches are highly distinctive and closely simulate those of Rosemary.

99a. S. RHOMBIFOLIA R. & P. PERU—ANCASH: Prov. Santa, Lomas de Mongon near San Rafael, between Casma and Huarmei, *Stork, Horton and Vargas 9177*; same, Lomas de La Chay, 40 km. north of Barranca, *Stork, Horton and Vargas 9213*.

110. S. SAGITTATA R. & P. PERU—LA LIBERTAD: Prov. Santiago de Chuco, above Cachicadan, 2800 m., *Stork and Horton 9958*.

111. S. RHODOSTEPHANA Epling. PERU—AYACUCHO: Ocros, Pajonal to Ayacucho, 9000 ft., *Balls 6925*. A more accurate description of the corolla is now possible. The tubes vary from 22–25 mm., the upper lip from 7–9 mm., the lower lip being about twice as long. The stamen connective is 30–40 mm. long. The color may vary from pink to "blue or pale mauve."

118. S. MENDAX Epling. GUATEMALA—JALAPA: Between Quisiltepeque and Potrero Carillo, 1800 m., *Steyermark 33073*. ZACAPA: Sierra de las Minas, 1000–1500 m., *Steyermark 29739*.

21A. Gentryana

Herbae perennis sat crassae pilis ramosis molliter pubescentes foliis sat magnis ovatis petiolatis; floribus pedicellatis, tribus in verticillastris bracteis parvis caducis subtentis in spicas axillares vel spremas paniculatas confertis; calycum parvorum truncatorum labia superiore 5-venis; corollarum roseo-purpurearum tubo recto intus nudo quam calyces duplo longiore, labia superiore erecta vix galeata, inferiore latiore vix tamen quam superior longiore; staminibus ad fauces positis ultra labiam superiorem exsertis, gubernacula integro vel ad connexum dente extenso ornato; styli glabri ramo postice subnullo.

122b. **S. trichostephana** Epling, sp. nov. (*Gentryana*). Herba perennis crassa altitudine ad 2 m., ramis pilis ramosis sat dense vestitis internodiis speciminis suppetentis quam folia brevioribus; foliorum laminis ovatis, 8–11 cm. longis, 4–7 cm. latis, crenato-serratis, pagina superiore pilis ramosis parvis sparse conspersa, inferiore cinerea; petiolis 2–2.5 cm. longis; spicis gracilibus sat confertis 5–6 cm. longis, inferioribus axillaribus, superioribus paniculatis; floribus tribus in verticillastris bracteis caducis parvis subtentis, pedicellis 3 mm. longis elatis; calycibus florentibus 2.5 mm. longis, subtruncatis, pilis simplicibus subappressis hirtellis in maturitate non visis; corollarum roseo-purpurearum tubo 5 mm. longo, recto, labia superiore 2.5 mm. alta, inferiore aequilonga rotunda; staminibus ultra labiam superiorem 3 mm. exsertis; gynobasis cornu quam nuculae triplo longiore.

MEXICO—SINALOA: Puerto a Tamiapa, 6–8.III.1940, *Gentry 5846* (TYPE, Univ. Calif., L. A.).

This remarkable plant does not resemble any other continental section in floral structure, but suggests most nearly the section *Wrightiana* of Cuba and Haiti. That section differs however in the fact that the upper lip of the calyx is 3-veined, the lower lip of the corolla is longer than the upper, the corolla is blue and the pubescence simple.

In the Key to the Sections (p. 6, line 34) this section would be sought near *Hastatae*, *Micranthae* and *Rhombifoliae*. That portion of the Key should therefore be emended to read as follows:

"CC. Calycum labia superior 5–7 venis et ultra. D. Corollarum tubi 3.5–6 mm. longi; styli glabri ramus posticus saepius brevior etiam subnulli. E. Folia palaeforma; flores oppositi caerulei; herbae procumbentes colombianae (vide etiam *Blakea*) 18. *Hastatae*. EE. Folia ovata vel deltoideo-ovata; flores 2–6 in verticillastris et ultra. F. Herbae perennes sinaloenses crassae ramis pilis ramosis vestitis; corollae roseo-purpureae 21a. *Gentryana*. FF. Herbae parvae saepius annuae pilis simplicibus vesitae; corollae caeruleae. G. Stamina e labia superiore vix exserta; plantae boreali-americanae nisi insularum Galapagos 14. *Micranthae*. GG. Stamina sat exserta; plantae andinae 16. *Rhombifoliae*. DD. Corollarum tubi 10–43 mm. longi, etc., etc."

134. S. HIRTELLA Vahl. ECUADOR—TUNGURAGUA: Mocha, Hacienda Yanagaca, 10,000 ft., 7.XI.1939, *Balls 7184*. "Leaves small, making a dense mat several feet across, on stems which creep along the ground and from which the flower stems stand upright." The bracts may be deciduous in fruit.

135a. (149) S. PRAECLARA Epling, Rep. Spec. Nov., Beih. **85**: **121**. **1936**. A shrub or perennial herb as much as 2 m. tall, its stems glandular and viscid with spreading hairs of varied length, as much as 2 mm. long; leaf blades membranous, commonly 6–12 cm. long, 5–12 cm. broad, mostly deltoid in outline, somewhat acuminate at the apex, broadly and definitely cordate at the base, or the upper ones deltoid-lanceolate and subtruncate, their margins irregularly and rather coarsely crenate or serrate, both surfaces bright green and nearly glabrous, thinly glandular on the upper surfaces with spreading hairs, and along the veins beneath; bracts fugacious, 3–5 mm. long, ovate-acuminate, hispidulous; flowers several in each verticil, the glomerules at length 1–3 cm. distant; flowering calyces 8–11 mm. long, often reddish toward the tips, glandular with spreading hairs similar to those of the stems, 12–13 mm. long at maturity, the lower calyx teeth partially connate, the mature pedicels 5–6 mm. long; corolla bright clear crimson, its tube 14–25 mm. long, bearing an elliptical dense areole of stiffish short hairs on the lower side above the ovary, the upper lip 7–8 mm. tall, the lower about twice as long, the middle lobe ample; stamens seated about 3 mm. below the orifice, the filaments 7–9 mm. long, the connective 30–32 mm. long, the rudder 12–13 mm. long, bearing a sharp spreading tooth 1.5 mm. long, which projects from the throat.

Previously known only from the type, collected by Pearce in Mecoya Valley. The following specimens have permitted a more accurate description of this species and, with adequate material of the corollas, its assignment to Sect. *Mineatae* rather than Sect. *Cylindriflorae*. This species not improbably has horticultural value. According to Eyerdam it is sweetly scented with the odor of lemon.

Bolivia—cochabamba: Prov. Mizque. Vilavila, 2500–2600 m., *Eyerdam 25079, 25022, 25329;* 3 km. south of Cochabamba, 2800 m., *Eyerdam 24929, 24931;* 1 km. northwest of Vilavila, 2500 m., *Eyerdam 24974.*

The Key to the Sections (p. 7, line 11) should be amended to read as follows:

II. Plantae Argentinae et Bolivianae; bracteae deciduae .... 28. *Mineatae.*

The Key to section Mineatae should read as follows:

Calyces florentes 14–17 mm. longi; corollarum tubi 23–28 mm. longi; plantae argentinae .... 135. *S. exserta.*
Calyces florentes 8–11 mm. longi; corollarum tubi 14–25 mm. longi; plantae bolivianae .... 135a. *S. praeclara.*

141. S. tubiflora Sm. Peru—ancash: Prov. Santa, Lomas de La Chay, 40 km. north of Barranca, *Stork, Horton and Vargas 9202.*

142. S. striata Benth. Peru—apurimac: Prov. Andahuaylas, Pincos, 2700 m., *Stork and Horton 10667.* "In fields everywhere; an annual herb to .5 m.; common eastward as far as Cuzco."

143. S. oppositiflora R. & P. Peru—cajamarca: Prov. Hualgayoc near Bambamarca, *Stork and Horton 10030.* The pubescence of the inflorescence and calyces is quite variable in this and in a second collection from Depto. Lima. The calyces and branchlets may be either glabrate, with a few eglandular hairs, or spreading-glandular.

154. S. Haenkei Benth. Bolivia—chuquisaca: Near Sucre, 8,500 ft., *Balls 6174.*

173. S. cinnabarina M. & G. Guatemala—jalapa: Volcan Jumay, 1800–2200 m., *Steyermark 32433;* Cerro Alcoba, near Jalapa, 1300–2200 m., *Steyermark 32538.*

177. S. ORBIGNAEI Benth. BOLIVIA—CHUQUISCA: Near Sucre, 8,500 ft., *Balls 6151*.

184. S. NITIDA (Mart.) Benth. MEXICO—GUERRERO: Sierrita near Galeana, 950 m., *Hinton 14997*. Known previously only from the type, collected at Juquila in Oaxaca.

189. S. MOCINOI Benth. GUATEMALA—SAN MARCOS: Volcan Tajumulco, 1300–1500 m., *Steyermark 37959*. The lips of the calyx tube of this specimen are scarcely 1 mm. long.

202a. **S. trifilis** Epling, sp. nov. (*Flocculosae*). Herba perennis caulibus ascendentibus altitudine ad (?) 60 cm., inter folia pilis extensis simplicibus eglandulosis sparse ornatis, inter flores extensis glandulosis dense vestitis; foliorum laminis ovatis 3–5 cm. longis, 2–3.5 cm. latis, in apice acutiusculis, in basi rotundatis (? interdum subcordatis), marginibus serrulatis, pagina superiore viride pilis simplicibus interdum ramosis sparse hirsuta, inferiore cinerea pilis ramosis sat tomentosa; petiolis 1–2.5 cm. longis elatis; floribus circiter 6 in verticillastris bracteis caducis subtentis, glomerulis caeruleis inter se 1–2.5 cm. distantibus in spicis interruptis 15–20 cm. longis dispositis; calycibus florentibus 6 mm. longis extus pilis extensis glandulosis ut videtur viscidis, labiis sat hiantibus acutis in maturitate paulo auctis; corollarum caerulearum tubo 6.5 mm. longo, labia superiore 3.5 mm. alta.

PERU—CAJAMARCA: Prov. Cuteros, Sucse River Valley west of Socota, 2800 m., *Stork and Horton 10105* (Univ. Calif., L. A., TYPE).

This species might readily be mistaken for *S. cuspidata,* known from Lima. However, the stamen structure and the branched pubescence of the leaves readily distinguish it. In habit and pubescence it also resembles some of the species of *Scorodonia*, a Mexican section, such for example as *S. melissodora*. However, the herbaceous rather than fruticose habit, the more spreading jaws of the calyces and the epapillate corolla tubes distinguish it from that group.

224a. S. CAPILLOSA Epling. A reconsideration of this species, together with *S. sapinea*, suggests the essential unity of the sections *Scorodonia* and *Urica,* although the extremes are rather diverse. Until more material is available for better understanding of the complex, it seems preferable to consider them as a single section, which would preferably take the name of *Scorodonia.* The Key to the Sections which refers to them can be bettered to read as follows (p. 11, line 37):

"KK. Corollae saepius caeruleae vel cyaneae, rarius albidae vel roseo-purpureae; caules vix decurrenti-villosi; plantae imprimis mexicanae. L. Corollarum caerulearum vel albidarum labia inferior quam galea longior (vide etiam 59a *Nivalis;* corollae albae albo-pilosae). M. Folia modo oblongo-lanceolata vel linearia et bractea saepius decidua modo ovata tamen bractea saepius perstata; corollarum tubi intus nudi (*S. leptophylla* et *similis* exceptae) 46. *Farinaceae.* MM. Folia ovata vel deltoidea (*S. occiduae* oblongo-lanceolata); bractea decidua; corollarum tubi intus ad basim rugis binis vel papillis ornati, rarius nudi 43. *Scorodonia.* LL. Corollarum cyanearum vel roseo-purpurearum labia inferior quam galea subaequilonga vel brevior. M. Folia deltoidea, bullulata; corollarum tubi albi, labiae cyaneae 52. *Atratae.* MM. Folia ovata-elliptica in basi angustata (*S. festivae* rotundata); corollae vix bicolores. 59. *Maxonia.*"

Following is a suggested modification of the Key to *Scorodonia* to include the species of *Uricae* (p. 167, line 18 seq.):

Corollarum tubi 5–15 mm. longi; folia pilis longioribus saepius appressis frequenter glandulosis hirsuta, interdum glabra.
  Folia plerumque 4 cm. longa et ultra; petiolis saepius plus quam 1 cm.; ramulorum pili magnam partem 2–3 mm. longi.
    Corollarum tubi 5–7 mm. longi.
      Corollarum tubi intus ad basim rugis binis ornati; plantae San Luis Potosi, Hidalgo, Mexico, Guanajuato, Tlaxcala et Puebla .... 224. *S. amarissima.*
      Corollarum tubi intus nudi; plantae Oaxaca et Michoacan. 224a. *S. capillosa.*
    Corollarum tubi 8–15 mm. longi; plantae guatemalenses vel mexicanae.
      Folia utrimque patentim hirsuta et subtus saepius tomentosa; plantae guatemalenses .... 225. *S. Urica.*
      Folia utrimque glabra et viridia, nisi ad venas sparsissime pilosa; plantae mexicanae (Guererro) .... 225a. *S. sapinea.*
  Folia plerumque minus quam 4 cm. longa; petioli rarius plus quam 1 cm.; ramulorum pili magnam partem 1–2 mm. longi.
    Ramuli utrimque pilis glandulosis plus minusve vestiti etc. etc.

225. S. URICA Epling. GUATEMALA—CHIQUIMULA: Montaña Nonojá, near Camotán, 600–1800 m., *Steyermark 31697;* Volcan Quezaltepeque, 1500–2000 m., *Steyermark 31493.* JALAPA: Zapote, near San Pedro Pinula, 1500 m., *Steyermark 32958;* Montaña Miramundo, between Jalapa and Lago Ayarza, 2000–2200 m., *Steyermark 32794;* Potrero Carrillo, 13 mi. N. E. of Jalapa, 1500–1700 m., *Steyermark 33129.*

225a. **S. sapinea** Epling, sp. nov. (*Uricae*). Suffrutex altitudine ad 1.5 m. ramulis gracilibus fere glabris tamen pilis longioribus extensis vel recurvis sparse conspersis tamen inter flores brevibus glandulosis et crassioribus dense obsitis; foliorum laminis cordato-ovatis, 6–12 cm. longis, 4–8 cm. latis, in apice breviter et abrupte acuminatis, in basi saepe obliquis, marginibus serratis, pagina superiore fere glabra breviter et sparse hirtella inferiore ad venas pilis longioribus appressis sparsissime ornata, petiolis 3–10 cm. longis, villosis; floribus 6 in verticillastris sat densis bracteis caducis parvis subtentis, glomerulis inter se 1–2 cm. distantibus in spicis interruptis 15–20 cm. longis strictioribus positis; calycibus florentibus purpureis 7–8 mm. longis extus pilis glandulosis brevioribus extensis et paucis crassioribus obsitis, in maturitate paulo auctis; labia superiore 3–5–7-venis; pedicellis 5–6 mm. longis elatis; corollarum violacearum tubo 9–12 mm. longo intus papillis quatuor ornato, labia superiore 4.5–5.5 mm. alta, inferiore duplo longiore.

MEXICO—GUERRERO: Teotepec, distr. Mina, 3375 m., in open pine and fir forest, 6.XI.1939, *Hinton 14798* (TYPE, Univ. Calif., L. A.)

The nature of the stamen connective is somewhat variable. It is usually almost entire or with a slight tooth toward the middle. Occasionally, however, the tooth appears to be somewhat assurgent, in which case the species might be sought under *Fernaldia* (p. 10), from which it may readily be distinguished in a number of ways. If only those calyces which have a 3-veined upper lip are examined, the species would be sought under *Polystachyae*, from which it would be at once distinguished by the size of the corolla, the corolla tubes of that section rarely being over 6 mm. long. See 224a, this paper, for key.

228. S. CORDATA Benth. URUGUAY—SALTO: San Antonio, en cuchillas pedregosas, XI.1937, *Orihuela* (*Rosengurtt 2682*). This species has been known previously only from Rio Grande do Sul.

243a. S. JACOBI Epling. MEXICO—GUERRERO: Yesceros-Cruz Pacifica, 3050 m., *Hinton 14891*.

253. S. RYPARA Briq. This species, predominantly of northwestern Argentina and adjacent Bolivia, may be represented by *Eyerdam 24937*, collected at Cochabamba. Cochabamba, however, is the type locality of *S. platystoma* Epl., known only from specimens collected there by *Bang* (*no. 2032*) and Holway (*no. 386*). The habit, pubescence and flower size of Eyerdam's specimen strongly suggests *S. rypara*, save in the fact that the leaves tend to be deltoid. Whether both supposed species occur there, whether the present specimen is a variant of *S. platystoma* or whether these species are in fact one, is obscure.

267. S. SHANNONI J. D. Smith. GUATEMALA—CHIQUIMULA: Montaña Castilla, near Montaña Cebollas, 3 mi. S. E. of Quezaltepeque, 1200–1500 m., *Steyermark 31220*. On Socorro Mountain between Finca San José and Montaña Nube, 1200–1700 m., *Steyermark 30924*.

273. S. SACCULUS Epling. MEXICO—NUEVO LEON: Below Alamar, about 15 mi. S. W. of Galeana, *Mueller and Mueller 1133*.

281. S. FILIPES Benth. (*S. decora* Epling in Rep. Spec. Nov., Beih. **110**: 222. 1939.) MEXICO—GUERRERO: Armenia Lagunas, 1900 m., Mina, *Hinton 9762;* Puerto Rico, 1800 m., *Hinton 14980;* Chilacayote—Carrizal, 1400 m., *Hinton 14921;* Yesceros—Cruz Pacifica, 2550 m., *Hinton 14900*. The three most recently collected specimens demonstrate the unity of these species, for they seem clearly to connect the two types, separable chiefly because of the narrower leaves, smaller and reflexed flowers of *S. decora*. The flowers may be either white or pale blue.

282. S. PLURISPICATA Epling. MEXICO—MICHOACAN: Mt. Tancitaro, 2850 m., *Hinton 15527*. Although more closely allied by habit to species of *Polystachyae*, as indicated previously, the corolla tubes of this well-marked species are frequently epapillate. Such plants would be sought under *Angulatae*. The styles of the present specimen are glabrous, an unusual condition in the small, blue-flowered sections.

293. **S. pineticola** Epling, sp. nov. (*Carneae*) Herba (?) perennis altitudine 60 cm., caulibus superne pilis decurvis minutis magnam partem eglandulosis pubescentibus, internodiis quam folia brevioribus; foliorum laminis late ovatis, 5–8 cm. diametro, in apice breviter acuminatis, in basi subtruncatis vel leniter cordatis, marginibus convexioribus, serratis, pagina superiore hirtella, inferiore praesertim ad venas pilis crassioribus articulatis sparse villosa; petiolis 5–7 cm. longis; floribus 3–6 in verticillastris bracteis caducis subtentis, in spicis confertioribus 5–15 cm. longis dispositis, glomerulis inter se 5–10 mm. distantibus; pedicellis 3–5 mm. longis; calycibus florentibus tenuibus membranaceis viridibus 5 mm. longis, in maturitate 7 mm. longis, extus glabris, nullomodo glandulosis; corollarum albarum tubo 9 mm. longo, labia superiore 4 mm. alta.

MEXICO—VERA CRUZ: Lomagrande, Mt. Orizaba, 8700 ft., 27.VIII.1938, *Balls 5368* (USNH, TYPE).

In the amended key to the section this species would be sought near 294. *S. gracilis* from which it can be distinguished by the curled eglandular pubescence of the stems, the relatively broad leaf blades, the (? always) white corollas and glabrous, thin calyces which are greenish rather than tinged with red.

294. S. GRACILIS Benth. GUATEMALA—QUEZALTENANGO: Volcan Zanil, 2500–2800 m., *Steyermark 34612*. Calyces nearly 10 mm. long at maturity, 6 mm. in flower. Corolla tubes 12 mm. long, the upper lip 5.5 mm. tall. Otherwise like typical specimens gathered in this vicinity (*Standley 67330*). Specimens recently collected by *Hinton* (*no. 15397*) in Guerrero near Galeana between Piedra Ancha and Tres Cruces may be a white flowered form of this species. The corolla tubes are 11 mm. long, however, and the leaf habit is somewhat different.

299. S. DEBILIS Epling. COLOMBIA—CUNDINAMARCA: Fusagasuga, 2100–2400 m., *Arbelaez and Cuatrecasas 6604;* Mun. Guasca, Paramo de Guasca, 300–3500 m., *Barriga 8093*. This presumed species may have the stems of the inflorescence and calyces minutely glandular, as well as quite glabrous. The habit of foliage is quite variable.

300. S. KILLIPIANA Epling. COLOMBIA—CUNDINAMARCA: Cord, Oriental, Paramo de Guasca, *Cuatrecasas 9445*. The inflorescence is glandular puberulent only.

310. S. ROSCIDA. A specimen collected by *Gentry* (*no. 3651*) in Sonora on Rio Mayo at Curohin apparently is referable to this species and raises the question of the identity of a more recent collection of his, (*no. 5828*) made in Sinaloa, Puerto a Tamiapa. That specimen is seemingly identical with the type of *S. mucidiflora* Fern., described from San Ramon, Durango, except that the villous pubescence of the inflorescence and calyces is almost wholly replaced by small capitate glands. At the same time *S. roscida* seems scarcely different save in flower size from *S. fallax* Fern., described from Tepic. This supposed species has a glabrate analog in Mexia's specimens from Jalisco (*no. 1683*). Furthermore, *S. remissa* Epl., described from Jalisco (*Mexia 1559*) is very similar to *S. fallax*, and specimens recently gathered in Michoacan by *Hinton* (*nos. 12128, 12480, 12357, 12208*), which seem referable to that species, are in turn scarcely to be separated from *S. mucidiflora*. It seems probable, therefore, that *S. mucidiflora* Fern., *S. fallax* Fern., and *S. remissa* Epl. are all referable to *S. roscida* Fern, and form a species which ranges from Durango and southern Sonora to Michoacan. In this species the pubescence of the inflorescence varies from nearly glabrous (*Mexia 1683*) to finely glandular (*Gentry 5828*) or commonly to villous, as in the remaining specimens. The bracts are either deciduous or subpersistent. More abundant collections are needed to reach a decision.

312. S. ARTHROCOMA Fern. MEXICO—VERA CRUZ: Jalapa, San Miguel, 6,500 ft., *Balls 4724*. This specimen appears to be nearest to *S. arthrocoma*, known only from the type locality in Hidalgo, to which it is similar in general habit, the habit of the flowers and pubescence. It has smaller leaves, rounded at the base, and smaller flowers. Jalapa is the type locality of *S. xalapensis*, but the present specimen seems scarcely to be that species.

312b. S. FLACCIDIFOLIA (Angulatae) Fern. in Proc. Am. Acad. **43**: 66,

1908. Type: Mexico—Hidalgo: barranca below Trinidad Iron Works, *Pringle 10298* (Gray).

Herba verisimiliter suffruticosa ramis gracilibus superne hirtellis et plus minusve glandulosis; foliorum laminis sat tenuibus pulchre ovatis, 6–9 cm. longis, 4–6 cm. latis, supra medium acuminatis, etiam subcaudatis, in basi sat rotundatis et cordatis, marginibus serratis, paginis ambabus sparse hirtellis; petiolis gracilibus plerumque 3–6 cm. longis; floribus tribus in bracteorum caducorum axillis, interdum solitariis et oppositis, pedicillis gracilibus 4–5 mm. longis elatis, in racemis laxis 6–8 cm. longis dispositis; calycum florentium tubo 7 mm. longo, extus glanduloso-puberulo, labiis acuminatis; corollarum cyanearum tubo 13–14 mm. longo, galea 9–10 mm. alta.

Mexico—Hidalgo: Barranca below the Trinidad Iron Works, 6.IX.1906, *Pringle 10298.*

Similar to *S. cyanantha* but the leaves cordate at the base and the flowers somewhat larger and of different conformation. The key to this section is in urgent need of revision, but the material at hand is as yet hardly sufficient. In the present key, this species would probably be sought near *S. myriantha.*

314b. **S. trichopes** Epling, sp. nov. (*Angulatae*). Herba suffruticosa ut videtur ramulis gracillimis glaberrimis; foliorum laminis ovatis, 2.5–4 cm. longis, supra medium acuminatis, in basi rotundatis, marginibus serratis, pagina superiore hirtella vel glabra, inferiore glaberrima; petiolis filiformibus 1.5–2.5 cm. longis; floribus tribus in verticillastris bracteis caducis subtentis, pedicellis gracilibus 3–4 mm. longis elatis; glomerulis laxis inter se 1–2 cm. distantibus in spicis interruptis gracilibus laxis 15–20 cm. longis dispositis; calycibus florentibus 6 mm. longis, sparsissime hirtellis, in maturitate paulo auctis; corollarum rosearum tubo 10 mm. longo, labia superiore 4.5 mm. alta.

Panama—Chiriqui: in vicinity of Bajo Chorro, 1900 m., *Woodson and Schery 693* (Univ. Calif., L. A., TYPE). Similar in aspect to *S. languidula* of Michoacan and Guerrero, but more glabrous, with larger flowers and deciduous bracts.

339a. **S. cyanicalyx** Epling, sp. nov. (*Angulatae*). Herba perennis altitudine ad 1 m. ramis superne pilis parvis appressis hirtellis, internodiis elongatis quam folia longioribus; foliorum laminis amplis, late ovatis, 8–11 cm. longis, 7–8 cm. latis, in apice breviter acuminatis, acutissimis, in basi rotundatis et ad petiolos abrupte et anguste cuneato-angustatis, marginibus convexioribus, serratis, pagina superiore fere glabra, hirtella, inferiore pilis parvis albo-tomentosa; petiolis 3–4 cm. longis; floribus pluribus in verticillastris, bracteis caducis subtentis, glomerulis inter se 1–5 cm. distantibus in spicis interruptis atro-cyaneis dispositis; calycibus florentibus atro-cyaneis, hirtellis, fere glabris, circiter 9 mm. longis, in maturitate 12 mm. longis 10 mm. latis, labiis hiantibus, acuminatis; corollarum pallide caerulearum tubo sat ventricoso, 12 mm. longo, labia superiore 4–5 mm. alta.

Allied to *S. amplifrons* of Bolivia from which it differs chiefly in the larger corollas and proportionately broader leaves; suggests *S. stachydifolia* (*Malacophyllae*) in habit, but the upper lip of the calyx is definitely 3-veined.

Peru—Apurimac: Prov. Abancay, Ampuy, 2400–3200 m., 12.II.1939, *Stork, Horton and Vargas 10618* (Field Mus., TYPE).

345. S. AMETHYSTINA J. D. Smith. COLOMBIA—BOYACA: Alto carretera sobre Puente de Boyaca, 2800 m., *Arbelaez and Cuatrecasas 8077*. The upper lip of the calyces is sometimes 5-veined. Furthermore, a fact which I failed to note, the stamens are seated between the middle of the corolla tube and the throat. The general key should accordingly be modified to read as follows (p. 8, line 32):

"H. Stamina vel ad tubi medium vel inter tubi medium et fauces posita. I. Corollae caeruleae infra medium patentim invaginatae 58. *Ampelophyllae*. II. Corollae rubrae vel coccineae integrae 29. *Rubescentes*," and on p. 11, line 5:

"E. Stamina inter corollae tubi medium et fauces posita. F. Corollae labiae breves inferioris lacinia media incurvo-concava (vide etiam *Albolanatas* et *Rubescentes*); tubi integri 91. *Secundae*. FF. Corollae caeruleae labia inferior quam superior longior et patentim deflexa 58. *Ampelophyllae*."

59a. Nivalis

Suffrutex ramis gracilibus internodiis sat elongatis foliis deltoideo-ovatis petiolatis; floribus 3–6 in verticillastris bracteis caducis subtentis in spicis interruptis sat confertis dispositis; calycum labia superiore obtusa imprimis 3-venis, interdum 5-venis, inferior pro rata breviore acuminata; corollarum nivearum extus dense albo-hirsutarum tubo intus ad basim papillis quatuor ornato et sub papillas paulo constricto, labiis subaequilongis; staminibus in galea inclusis in faucibus positis, gubernaculo ad connexum dente retrorso ornato; stylo utrimque hirsuto, ramo postico longiore.

351b. **S. Leninae** Epling, sp. nov. (*Nivalis*). Suffrutex altitudine ad 2 m. ramulis pilis extensis vel subretrorsis praesertim ad sulcos ornatis; foliorum laminis deltoideo-ovatis 4–7 cm. longis, 3–5 cm. latis, in apice leniter acuminatis, in basi rotundato-truncatis, paginis ambabus pilis rectis praesertim ad venas sparse conspersis, marginibus serratis; petiolis villosis 1.5–5 cm. longis; calycibus florentibus 8–9 mm. longis ad venas pilis rectis sparse conspersis; corollarum nivearum extus albo-pilosarum tubo 12 mm. longo, labia superiore 8–9 mm. alta, inferiore subaequilonga; staminibus 11–12 mm. longis.

MEXICO—GUERRERO: Yesceros-Cruz Pacifica, 2900 m., in pine-oak forest, 26.XI.1939, *Hinton 14897* (TYPE, Univ. Calif., L. A.).

In the key to the sections this species would probably be sought near *Maxonia*. The key should be amended to read as follows (p. 8, line 1):

"E. Corollarum tubi 6–13 mm. longi; plantae mexicanae et centrali-americanae. F. Folia utrimque angustata; corollae caeruleae vel roseae 59. *Maxonia*. FF. Folia in basi truncato-rotundata; corollae albae albo-pilosae 59a. *Nivalis*. EE. Corollarum tubi 15–27 mm. long (*S. purpurae* interdum 10–12 mm. longi; vide etiam species colombianam, *S. erythrostoma*). F. Corollae roseo-purpureae vel coccineae. G. Folia in basi saepius rotundata, rarius angustata; 87. *Purpureae*. GG. Folia in basi ad petiolos angustata vel extenuata; corollae coccineae; plantae colombianae 83. *Killipiana*. FF. Corollae cyaneae; plantae guatemalenses 83a. *Latentiflorae*."

If this species is sought in the category in which the upper lip is 5-veined, see under species 224a (p. 560, this paper).

I quote from a letter of transmittal from Mr. James C. Hinton: "If there are any new Salvias in the lot, and if it would be in keeping with the dignity of the subject, I should like to ask you to name a Salvia for my black mule 'Lenina,' which has been in the field for ten years now and has played an indispensable part in the finding of a majority of our new Salvias. Both my father and myself you have already honored. Would it not therefore be just, I ask, to send Lenina's name also down to posterity on some new Salvia?"

I have carefully searched the pages of the International Rules to learn whether there is any prohibition against naming Salvias after mules, but I find none. And what is more deserving of commemoration than the dignity of long and faithful service to science even though it be somewhat unwitting—or sometimes unwilling? Long life to Lenina!

354. S. MEXICANA L. MEXICO—GUERRERO: Yesceros-Cruz Pacifica, 2850 m., Mina, *Hinton 14889;* Petlacala—Buenavista, 2600 m., Mina, *Hinton 14878.* These specimens are apparently referable to the form which was named *S. lupulina* by Fernald. The calyces are broader and the lips relatively shorter. The corollas are somewhat stouter. Branched hairs are frequently seen. The nature of this complex is uncertain, and until much more herbarium material is available for comparison, no certain conclusions can be made. It appears probable, however, that three entities are involved.

379a. **S. betulaefolia** Epling, sp. nov. (*Erythrostachys*). Frutex pulcher ramulis pilis plus minusve retrorsis cinereo-pubescentibus; foliorum laminis deltoideo-ovatis frequenter habitus Betulae, sat tenuibus, 2.5–6 cm. longis, 2–4 cm. latis, supra medium saepius acuminatis et in apice acutis, in basi saepius truncatis, irregulariter dentato-crenatis paginis ambabus pilis extensis sparse pubescentibus; petiolis 1–2 cm. longis; floribus oppositis in paniculis paucifloris brevibus bracteis parvis coloratis perstatis subtentis dispositis; calycibus florentibus pulchre coccineis 16–20 mm. longis, sparse hirtellis, in maturitate paulo auctis subinflatis et infra medium angustatis; corollarum pulchre coccinearum tubo 35–37 mm. longo, labia superiore 16–17 mm. alta.

MEXICO—DURANGO: Tejamen, 21–27.VIII.1906, *E. Palmer 477* (TYPE, USNH); Tepehuanes, 4–25.VI.1906, *E. Palmer 292;* Santiago *Papasquiaro,* 1896, *E. Palmer 404.* CHIHUAHUA: Mojarachic, 6900 ft., 30.VIII.1939, *I. Knobloch 5833.*

A member of the section *Erythrostachys* (no. 379a) and formerly included by me in *S. Regla.* It is more nearly intermediate between *S. Regla* and *S. Sessei.* It may be distinguished from *S. Regla* by the acuminate leaves which are proportionately longer, those of *S. Regla* being broadly deltoid or even reniform, by the more irregular serratures of the leaf margin and by the pubescence, which is not only more abundant but coarser in quality. Just as the leaves of *S. Regla* suggest those of *Populus tremuloides,* the leaves of *S. betulaefolia* suggest those of *Betula alba.*

381. S. SESSEI Benth. MEXICO—MICHOACAN: Zitacuaro to Cayota, 1840 m., *Hinton 13160.*

389. S. SIGUATEPEQUENSIS Standl. GUATEMALA—CHIQUIMULA: Montaña Nube (Volcancitos), southeast of Concepcion de las Minas, 1500–1700 m., *Steyermark 30912; 30913.* Partly intermediate between this species and *S.*

Karwinskii. The latter, in typical form, has been collected in Guatemala and it is entirely possible that *S. siguatepequensis* is only a southern phase of it. The calyces are hispidulous and glandular.

390. S. KARWINSKII Benth. MEXICO—CHIAPAS: Volcan Tacana, Chiquihuite, 2800 m., *Matuda 2826.* GUATEMALA—JALAPA: 6 mi. south of Miramundo, Montaña Miramundo, 2000–2500 m., *Steyermark 32705; 32757.* JUTIAPA: Volcan Suchitan 2050 m., *Steyermark 31900.* SAN MARCOS: Volcan Tacana, 2200–2500 m., *Steyermark 36040* (an epiphyte on lower trunk of forest tree).

392. S. WAGNERIANA Polak. GUATEMALA—CHIQUIMULA: Montaña Nube (Montaña Volcancitos), southeast of Concepcion de las Minas, 1500–1700 m., *Steyermark 30916.*

The general key to sections (p. 11, line 32) should be modified to read as follows:

J. Plantae peruvianae; corollarum tubi 13–23 mm. longi 64. *Pavonia.* JJ. Plantae mexicanae vel centrali-americanae. K. Corollarum caerulearum tubi 3.5–15 mm. longi 43. *Scorodonia.* KK. Corollarum coccinearum tubi 18–25 mm. longi 70. *Cardinales.*"

391. S. HOLWAYI Blake. GUATEMALA—CHIQUIMULA: Rio Taco, between Chiquimula and Montaña Barriol, 500–1200 m., *Steyermark 30627.* ZACAPA: Sierra de las Minas, 1000–1500 m., *Steyermark 29665.* The leaves of this variable, but readily recognized species, may be as much as 13 cm. long and 8 cm. broad, the petioles being as much as 7 cm. long. The corolla tube may be as short as 15 mm.

401a. S. GRAVIDA Epling. MEXICO—MICHOACAN: Mt. Tancitaro, 2300 m., *Hinton 15677.* The flowers of this species are a beautiful rose-purple. Those of the present specimen appear to be more bluish purple, perhaps due to the accidents of pressing. It is a handsome subject and deserves introduction into our gardens.

410. S. DOMBEYI Epling. PERU—CUZCO: Prov. Paucartambo, near Marcachea, 2400 m., *Vargas 11106.* Described on the label as a tree 3–5 m. tall.

411. S. SCANDENS Epling. PERU—CUZCO: Prov. Quispicanchi, Marcapata, near Chile-Chile, 2000–2500 m., *Vargas 9678.* The type, collected in the same place was said by Weberbauer to be scandent. Apparently it is not always so. It is difficult to determine from the material at hand, but the lower lip of the corolla may be the longer. The species is doubtfully referable to section *Longiflorae.*

420. S. LATENS Benth. (*S. laurifolia* Epling in Rep. Spec. Nov. Beih. **85**: 102. 1936.) COLOMBIA—EL CAUCA: Popayan, Tiembio en Hatoviejo, 1800 m., *Arbelaez* and *Cuatrecasas 6067.* CUNDINAMARCA: Dintel (Facatativa-La Vega), 2700–2800 m., *Arbelaez and Cuatrecasas 5297.* Salto de Tequendama, 2440 m., *Cuatrecasas 8184.*

These proposed species are separable chiefly on the basis of the villous pubescence of the stems and calyces of the former, together with the fact that the flowers are axillary. That both criteria are variable in the type locality is shown by *no. 6067,* and it accordingly seems preferable to consider the species synonymous. Nevertheless, the plants of Cundinamarca appear to be constantly glabrous. The corollas of *Cuatrecasas 8184* are larger than specimens previously referred here, including the type from the same locality. The corolla tubes are as much as 21 mm., the upper lips 19 mm. and the lower lips 12 mm. long.

83a. Sect. Latentiflorae.

Frutices foliis anguste ovatis vel ellipticis in basi angustatis, subcuneatis, breviter petiolatis; floribus in foliorum axillis solitariis in foliis latentibus, ut videtur nullomodo in spicis dispositis; calycibus glabris, labiis acuminatis, superiore 3-venis; corollarum cyanearum tubo superne gradatim ampliato ad basim papillis binis majoribus assurgentibus et binis minoribus retrorsis ornato, nullomodo invaginato, labia superiore erecta, inferiore subaequilonga; staminibus in galea inclusis; stylo piloso, ramo postico longiore; gynobasis cornu ovarium paulo superante. Plants of Guatemala. TYPE SPECIES: *S. opertiflora.*

An amended portion of the key to the sections which includes this section will be found under species 351b (page 565, this paper).

422a. **S. opertiflora** Epling, sp. nov. (*Latentiflorae*). GUATEMALA. Dept. Chiquimula, Volcan Quezaltepeque, *Steyermark 31469* (Field Mus., TYPE.)

Frutex ramulis pilis extensis sat dense et molliter vestitis, internodiis quam folia brevioribus; foliorum laminis ovato-lanceolatis vel ellipticis, 8–9 cm. longis, 2.5–3.5 cm. latis, supra medium leviter acuminatis, in basi angustatis, marginibus serrulatis, pagina superiore viride, sparse hirtella, inferiore pallidiore, sparse villosula, venis purpureis; petiolis obscuris vix 1 cm. longis; floribus paucis axillaribus in foliis latentibus, pedicellis 4–5 mm. longis elatis; calycibus florentibus glaberrimis, pallidis, 12 mm. longis, labiis acuminatis, aequilongis, 4 mm. longis, superiore trivenis; corollarum atropurpurearum vel cyanearum tubo 18–21 mm. longo, habitus S. mexicanae, labia superiore 11–13 mm. alta, inferiore subaequilonga.

GUATEMALA—CHIQUIMULA: Volcan Quezaltepeque, 3–4 miles N. E. of Quezaltepeque, in open thickets, 1500–2000 m., 8.XI.1939, *Steyermark 31469.*

447. S. FLORIDA Benth. PERU—CAJAMARCA: Prov. Cutervo. Trail between Socota and Tambillo, forest of the Ceja de la Montaña, *Stork and Horton 10190.*

The flowering calyces are somewhat smaller (12–13 mm.) than described, and the corolla tube is about 26 mm. long, the stamens being correspondingly smaller. However, there is no doubt as to the identity.

454. S. EXCELSA Benth. GUATEMALA—SAN MARCOS: Volcan Tajumulco, 2300–2800 m., *Steyermark 36599.* First record for Guatemala of this species except the original specimen grown from seeds. See Bull. Torr. Club **67**: 533. 1940. MEXICO—GUERRERO: Paraje Javalin, 2500 m., distr. Mina, *Hinton 15416.*

DEPARTMENT OF BOTANY
UNIVERSITY OF CALIFORNIA AT LOS ANGELES

THE DEVELOPMENT OF THE PERISTOME IN AULACOMNIUM HETEROSTICHUM

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(WITH TWENTY-EIGHT FIGURES)

INTRODUCTION

The peristome is an interesting structure and in the systematics of mosses is considered to be of fundamental importance. The use of the peristome as a character in classification began in 1801 with the publication of Johann Hedwig's *Species Muscorum Frondosorum*, which has been selected as the starting point for nomenclature in the taxonomy of the true mosses. Since that time the establishment of the primary groups of the Bryales has been based alternately upon the peristome, a sporophytic structure, or upon the gametophyte. In recent times, however, owing especially to the influence of the works of Philibert (1884), Fleischer (1900–1922), Goebel (1906, 1930) and others, a more settled opinion has developed among the majority of the students of mosses that the peristome is of the greatest fundamental phylogenetic importance. In the most recent discussion on this subject, Dixon (1932) says, "For one thing it is quite clear that the main types of peristome among the Bryales are of great phylogenetic importance, and are more or less primitive, viz., the Nematodonteae and the Arthrodonteae, the latter divided into Haplolepideae and Diplolepideae. No part of our classification based on gametophyte characters must cut across these broad lines."

In view of this importance of the peristome in the study of mosses, it seems highly desirable that we should have a true concept of what this structure is and some appreciation of its variation in the different groups in which it occurs. Apparently, however, there is a general lack of understanding of what the peristome really is, and this is no doubt partly due to the scarcity of investigations dealing with its development. Furthermore, in some of the few works on this subject, incorrect interpretations add to the confusion.

It is the purpose of this paper to present an account of the embryonal development of a double-peristomate moss which is fairly representative of the diplolepidious Bryales. The main objectives are to show from what embryonic cell-layers a double peristome originates, how it is differentiated, the relation of its mature characteristics to its developmental history, and to correlate it with the peristome of a single-peristomate moss. It is done with the hope that it will lead to a better and wider understanding of this interesting and important structure and will stimulate further investigation.

HISTORICAL REVIEW

Although Hedwig was the first one to give us any knowledge of the structure of the moss capsule, his concept of the structure of the peristome was far from clear. The first work in which this subject was dealt with more adequately was that of Lantzius-Beninga (1847). The excellency of this contribution has made it a classic in the study of the morphology of mosses. He clearly showed what the peristome is composed of, its unity of plan, and its variation in the several groups which he considered. He was the first one to observe that the peristome is either composed of columns of whole dead cells or of only thickened portions of cells which remain after the surrounding delicate parts break away. Although he worked mainly with mature capsules in which the peristome is fully developed, he observed some of the developmental stages in such genera as *Ceratodon* and *Polytrichum*. Lantzius-Beninga observed the regularity of cell division in the outer region of the operculum, and called attention to the curious fact, which had previously been observed, that the number of parts of the peristome is always four or a multiple of four. He attributed this fact to the regularity of cell division.

Since the appearance of the work of Lantzius-Beninga, the investigations on the peristoma have made some progress along the following more or less distinct lines: (1) comparative morphology of usually mature peristomes from the viewpoint of relationship and phylogeny; (2) its function and behavior; (3) its embryonal development; and (4) its minute structure and chemical composition. Only the last two will be considered here.

The early contributions to our knowledge of the development of the peristome are included in the general investigations concerning the development of the sporophyte as a whole or of the capsule proper. The most important of these is the work of Kienitz-Gerloff (1878) on the development of the sporophyte in several members of the Bryales. He observed, as had Hofmeister (1851), that development proceeds from a two-sided apical cell which cuts off two rows of segments. Each of these segments then divides by an anticlinal wall which results in a column of quadrants of cells. By anticlinal and periclinal cell division the quadrants are further divided into an inner square of four cells and an outer layer of eight cells. The central square, which had been called the "Grundquadrat" by Kühn (1870), Kienitz-Gerloff named the "endothecium" and the outer peripheral layer the "amphithecium." He showed further that the peristome develops from the amphithecium and believed that the basic number of peristome teeth is four.

More special contributions to the development of the peristome were made by Goebel (1887) on *Funaria hygrometrica* Sibth. and *Polytrichum piliferum* Schreb., by Strasburger (1902) on *Mnium hornum* Hedw., and by Campbell (1905) on *Funaria hygrometrica*. All these accounts did not, however, include the early stages. An account of the development of the capsule of *Ceratodon purpureus* Brid. by Kuntzen (1913) contributed some facts concerning the early stages of the development of the peristome of this moss, although he was mainly concerned with the capsule proper.

The first and one of the few complete accounts of the embryonal development of a peristome in the Bryales is the work by Evans and Hooker (1913) on *Ceratodon purpureus*, a single-peristomate moss. This account is divided into two sections, the first dealing with the development of the peristomial layers and the second with the deposition of the thickenings. They found, as had Kienitz-Gerloff and Kuntzen, that a two-sided apical cell gives rise to two rows of semi-circular segments. After division by an anticlinal wall each pair of alternating segments forms a quadrant of cells. Further division by periclinal walls divides the quadrants into an endothecium of four cells and an amphithecium of eight cells. By periclinal division of the amphithecial cells, two concentric layers of eight cells each are formed, the inner of which becomes the "inner peristomial layer." The cells of the outer amphithecial layer then divide anticlinally and periclinally forming two layers of 16 cells each, and the inner of these becomes the "outer peristomial layer." The cells of this layer divide no further and the number of cells of which it is composed (16) determines the number of peristome teeth. The eight cells of the inner peristomial layer then divide by anticlinal walls in such a way that about three cells of this layer correspond to two cells of the outer peristomial layer. The cells of the outermost layer divide by less regular alternating anticlinal and periclinal walls so that about three layers are formed external to the outer peristomial layer. The innermost of these layers is composed of 32 cells so arranged that two cells correspond with each cell of the outer peristomial layer. The walls upon which deposition takes place to form the peristome teeth are the ones between the outer and inner peristomial layers. Further details concerning the differentiation of the teeth which results in their characteristic form and markings are fully discussed. Some consideration was also given to the statement made by Philibert (1888) that the peristome of a single-peristomate moss is homologous with the inner peristome of a double-peristomate one.

Since the work of Evans and Hooker, a few contributions have appeared dealing with other groups. For the purpose of determining the relationship of the Dawsoniaceae to the Polytrichaceae, Goebel (1906) investigated the peristome in *Dawsonia*. His conclusion that the anomalous peristome of this moss is fundamentally of the same type as in the Polytrichaceae has not, however, been generally accepted. For a similar purpose Goebel (1930) also investigated the development of the peristome in *Diphysium foliosum* Mohr. and *Buxbaumia indusiata* Brid. His conclusion was that the types of peristome present in these mosses indicate no close relationship to the Polytrichaceae as had been formerly supposed.

Working simultaneously but independently van der Wijk (1929) and Lorch (1931) made intensive investigations on the development of the peristome of *Polytrichum*. An additional contribution to the same genus has been made by Wenderoth (1931). Since the type of peristome present in *Polytrichum* has little in common with the type discussed here, a review of their contributions is not considered necessary.

In the work of Lorch, mentioned above, is also a brief contribution dealing with the peristome development of *Mnium cuspidatum* Leyss., a double-peristomate moss. While the early stages are not included, the development of the peristome of this moss up to the stage of the actual differentiation of the peristome teeth may be said to be essentially the same as that of *Ceratodon purpureus* as described by Evans and Hooker. However, since *Mnium* has a double peristome the actual formation of the teeth is quite different from that in *Ceratodon*. The walls upon which the deposit takes place to form the outer peristome are those between the "outer peristomial layer" of Evans and Hooker in *Ceratodon* and the next outer layer of twice as many cells. The inner peristome is formed from the slightly thickened walls between the "outer peristomial layer" and the "inner peristomial layer." In other words, the peristome of *Ceratodon purpureus* develops from the walls which are, with reference to their position, the same as those which develop into the inner peristome of *Mnium cuspidatum*. This fact recalls to mind the statement made by Philibert, mentioned above, concerning the homology of the inner peristome with the peristome of a single peristomate moss. Since in the formation of the double peristome in *Mnium cuspidatum* three layers of cells are involved, Lorch has modified the concept of the peristomial layers as understood by Evans and Hooker. He prefers to consider the innermost peristomial layer which contributes to the secondary thickening of the inner peristome as of a different type from the two succeeding outer layers which he designates as the true ("echte") peristomial layers.

The most recent work on the embryonal development of the peristome is that of Smith (1938) on *Funaria hygrometrica*. This differs from previous work done on this species in that the early stages are included.

The first study of the development of the minute structure of the peristome and its chemical composition was made by Derschau (1900). He concluded that the thickening of the cell wall is by apposition brought about through the activity of both cytoplasm and the nucleus. Cytoplasmic activity governs the first deposit which is largely cellulose and pectin. Later deposits, which are governed by the activity of the nucleus, show a strong reaction with sphagnol which, he concluded, is related to hygroscopic activity and antiseptic property. In the work on the peristome of *Mnium cuspidatum*, Lorch gave considerable attention also to its minute structure.

So far as is known no work has previously been done on the peristome development in *Aulacomnium heterostichum*. However, Lantzius-Beninga figured transverse and longitudinal sections of the mature peristome of *A. palustre* Schwaegr. (Tab. 62, Figs. 22, 23).

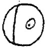
MATERIALS AND METHODS

Aulacomnium heterostichum (Hedw.) B. and S. is a common moss in the vicinity of Durham, North Carolina on shaded river bluffs, associated with other mosses, such as *Bartramia pomiformis* Hedw., *Cirriphyllum Boscii* (Schwaegr.) Grout, *Fissidens cristatus* Wils., and *Hypnum molluscum* Hedw. It is often found growing at the base of trees but it is not confined to this habitat. It is a spring-fruiting perennial which, like other such mosses, produces the sex organs in the spring nearly one year before the sporophyte reaches maturity. Fertilization takes place in the late spring. There seems to be little development of the embryonic sporophyte during the summer months. The sporophytes are first visible with a hand-lens in November. In North Carolina the most rapid growth of the sporophyte takes place during the late winter and early spring. Mature sporophytes are to be found about the middle of April. The peristome is double, consisting of an outer row of sixteen "articulate" teeth and an inner with alternating segments between which are located from two to four well developed cilia. According to the modern systems of classification, its taxonomic position is in the sub-class Bryales, order Eubryales Acrocarpi, and family Aulacomniaceae (Dixon 1932).

Plants were collected when the young sporophytes were first visible with a hand lens. The succeeding collections were made about two weeks apart until spring when collections were made at shorter intervals. Both transverse and longitudinal serial sections were made of the different stages of the developing capsule.

DEVELOPMENT OF THE PERISTOMIAL LAYERS

The early stages in the development of the sporophyte of *Aulacomnium heterostichum* are essentially the same as in all the Bryales which have been investigated. From the two-sided apical cell, diagonal cell walls cut off alternately semicircular segments (fig. 9). As division continues, the walls separating the older segments are bent down to a horizontal position, leaving the portions below the point where they join in a more or less vertical position (fig. 9). A transverse section of a very young sporophyte, or the tip of an older one, appears as a divided circle (fig. 1). Very soon, however, the alternating semicircular segments are divided radially by vertical walls resulting in a quadrant of cells in transverse view (figs. 2, 3). The cells of these quadrants are then divided by curved anticlinal walls into eight cells (figs. 4, 5). While there is some variation in the way these walls come in, the result is always the same.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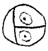
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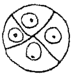
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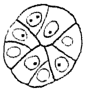
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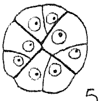
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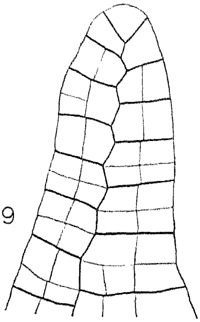
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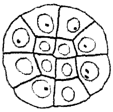
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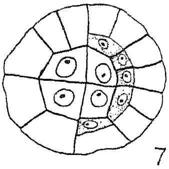
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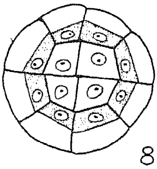
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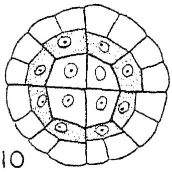
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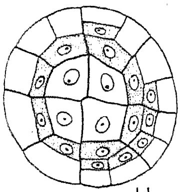
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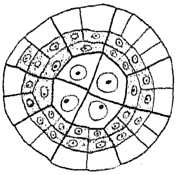
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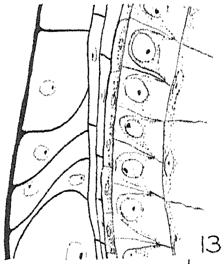
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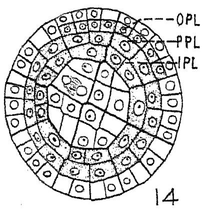

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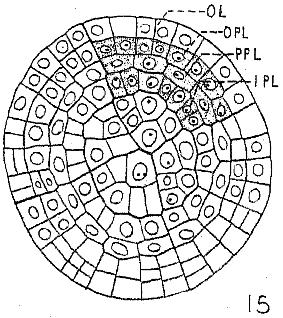

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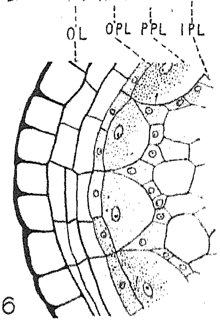

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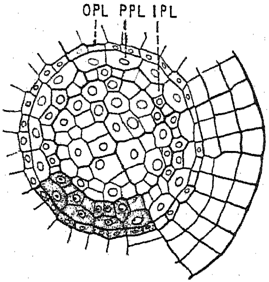

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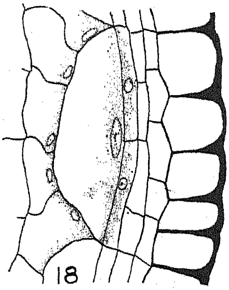
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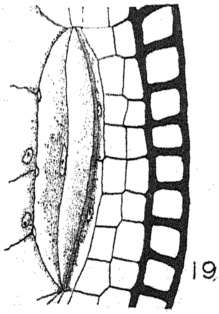
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The next step is periclinal divisions of the eight cells in such a way that a square of four cells is formed in the center surrounded by a layer of eight cells (fig. 6). The central group of four cells is the endothecium and the outer layer of eight cells the amphithecium. These two groups of cells are the fundamental embryonic layers in the sporophyte of mosses. Below the region of the operculum, the endothecium gives rise to the columella, the inner sporesac, and the archesporium; the amphithecium gives rise to the outer sporesac, the air spaces and the outside layers of the capsule proper (fig. 20). In the region of the operculum the endothecium consists of undifferentiated cells representing extensions of the regions in the capsule proper, but the amphithecium gives rise to the peristomial layers and the operculum. Since this paper is concerned mainly with the peristomial layers, not much attention will be given to the rest of the capsule.

Further development from the fundamental embryonic layers as shown in figure 6 proceeds with striking regularity in the three planes. Since the most important development takes place radially, most attention has been devoted to transverse sections. The regularity in development has two aspects. First, when a cell in a certain pericentral layer divides in a certain plane, all cells in that layer divide in the same plane at about the same time. Second, there is a regular alternation between periclinal and anticlinal divisions. That is, after a cell has divided periclinally the outer of the two daughter cells divides anticlinally. The result is that any layer of cells in the amphithecium has twice as many cells as the next inner layer. This regularity of cell division was called by Goebel the "Grundquadrat" or "fundamental square" method. As was pointed out by Kienitz-Gerloff, since all layers develop with this regularity of cell division from an original group of four cells, the result is that the number of cells in each pericentral layer will be a multiple of four. Furthermore, since the number of peristome teeth depends upon the number of cells making up a certain peristomial layer, the number of peristome teeth will also be of this series of numbers.

Going back to the fundamental embryonic layers, development is seen to proceed from them first by periclinal division of the cells in the amphi-

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Explanation of figures 1–19

All figures have been drawn with the aid of a camera lucida at the following magnifications: figures 1–25, × 415; figures 26–28, × 155.

The following abbreviations are used: OL, opercular layer; OPL, outer peristomial layer; PPL, primary peristomial layer: IPL, inner peristomial layer; SL, spore layer.

FIGS. 1–6. Successive stages in the development of the endothecium and amphithecium. FIGS. 7–8, 10–12, 14–17. Successive stages in the development of the peristomial layers. FIG. 9. Longitudinal section of a tip of a young sporophyte. FIG. 13. Longitudinal section of an immature peristome. FIG. 16. Transverse section of a peristome just before commencement of secondary thickening. FIG. 18. Commencement of secondary thickening of cell walls forming the peristome in the region of the annulus. FIG. 19. Advanced stage in the differentiation of the peristome.

thecium, resulting in two concentric layers of eight cells each (figs. 7, 8). The cells of the outer layer next divide anticlinally giving rise to 16 cells (fig. 10). This is followed by periclinal divisions in this layer giving rise to two concentric layers of 16 cells each (figs. 11, 12). Again the outer of these two layers divide anticlinally so that 32 cells are formed and these are divided periclinally into two outermost layers of 32 cells each (figs. 14, 15).

At this stage (fig. 15) the amphithecium is, therefore, composed of four concentric cell-layers. These layers will be referred to respectively, starting from the inside, as the inner peristomial layer (IPL), the primary peristomial layer (PPL), the outer peristomial layer (OPL), and the opercular layer (OL).

In the inner peristomial layer, which was originally composed of eight cells, the number of cells has increased by anticlinal divisions (fig. 15). The method of cell division and the ultimate number of cells in this layer will be discussed later. Since this layer contributes to peristome formation it was called by Evans and Hooker the "inner peristomial layer" and for the same reason has been so designated in this discussion.

The primary peristomial layer is composed of 16 cells which divide no further. They enlarge rapidly and their inside walls soon become distinctly convex (figs. 16, 17). This is, therefore, the first peristomial layer to appear conspicuously different from the other layers. For this reason and because, as will be shown later, the number of cells of which it is composed determines the number of teeth, it seems desirable to designate this layer as the *primary peristomial layer*. The cells of which it is composed will be referred to as the *primary peristomial cells*. This layer was called the "outer peristomial layer" by Evans and Hooker and the inner of the two "echte" peristomial layers by Lorch.

The cells of the outer peristomial layer are 32 in number and they divide no further. Their enlargement is almost entirely in a tangential direction. The cells of this layer also contribute to peristome formation, and for this reason it is called the *outer peristomial layer*. It is the outer of the two "echte" peristomial layers of Lorch. Since this layer does not participate in peristome formation in a single-peristomate moss such as *Ceratodon*, it was not given any special designation by Evans and Hooker.

The opercular layer, which at this stage consists of 32 cells, does not contribute to peristome formation. As in *Ceratodon* and other genera investigated, the cells of this layer continue dividing by a less regular alternation of periclinal and anticlinal divisions than is exhibited by the cells of the other layers, resulting in the formation of about three layers external to the outer peristomial layer (fig. 17). The outermost one of these differentiates into the operculum.

It must be realized, of course, that in the development of the sporophyte, growth soon ceases in the apical embryonic region, leaving the tip conical in form. This is partly responsible for the triangular shape of the peristome teeth.

THE DEVELOPMENT OF THE INNER PERISTOME

The inner peristome, also called the endostome, develops from the cell walls between the inner and the primary peristomial layers. As was stated above, the original eight cells of the inner peristomial layer at a certain stage (fig. 15) commence dividing anticlinally. The first division is usually such that one of the daughter cells is smaller than the other (fig. 15). The larger of the two then divides so that from the original cell three cells are formed which subtend two cells of the primary layer. This is exactly what Evans and Hooker found in *Ceratodon purpureus* but with this important difference, that in *Ceratodon* division goes no further while in *Aulacomnium heterostichum* division continues until eight or nine cells of the inner peristomial layer subtend two of the primary (figs. 16, 18, 19). In *Mnium cuspidatum*, Lorch found a similar arrangement. In *Funaria hygrometrica,* Smith shows only four cells of the inner layer subtending two of the outer. However, in the illustrations of this species given by Lantzius-Beninga (Tab. 63, Figs. 25, 27) the number varies from four to six, apparently depending upon the level of the operculum at which the sections are made.

As shown above, the inner walls of the primary peristomial cells become distinctly convex (fig. 17). The cause of this convexity is no doubt a combination of growth factors. Perhaps the most important of these is the formation of a larger number of cells subtending one primary peristomial cell in the inner peristomial layer than is formed in the outer peristomial layer. This at least partial explanation is supported by the fact that in such forms as *Ceratodon* and *Funaria,* in which the number of cells in the inner and outer peristomial layers subtending one primary peristomial cell is about the same, little or no convexity is exhibited by the primary peristomial cells. Other factors may be the position of the radial walls of the inner peristomial layer with reference to the radial walls of the primary peristomial cells, and the higher turgor pressure of the primary peristomial cells than that which obtains in the cells of the inner peristomial cells. One result of this convexity is the formation of wedge-shaped cells in the inner peristomial layer between the primary peristomial cells. The two walls of these wedge-shaped cells contiguous with portions of the inner walls of the primary peristomial cells form the "keels" of the "segments" of the inner peristome (figs. 16, 18, 19).

The commencement of deposition in the differentiation of the inner peristome is indicated by the migration of cytoplasm and nuclei of the inner peristomial layer toward the outer walls of these cells (figs. 16, 18, 19). Little if any secondary thickening apparently takes place on the contiguous inner walls of the primary peristomial cells. The deposit of the inner peristome is scanty and of homogeneous structure except in the upper portions where it is distinctly spicular (fig. 23). In the lower half of the inner peristome the deposit is continuous between the tangential walls, and the vertical rows of walls of this portion do not, therefore, separate. This basal portion of the inner peristome is known as the "basilar membrane" (fig. 28). In the upper half, however, no secondary thickening takes place at the junction of the tangential walls, which therefore separate in vertical strips except at the tips of the keels (figs. 23, 28). The narrow vertical strips between the keels are the "cilia," which vary in *Aulacomnium heterostichum* from two to four. No pores develop in the segments of this species like those noted by Lorch in *Mnium cuspidatum.*

On the outside of the lower half of the endostome, rows of curious button-like elevations are to be seen along the vertical walls between the radial horizontal walls (figs. 19, 28). So far as known these elevations have not been noted before in this or any other species.

THE DEVELOPMENT OF THE OUTER PERISTOME

The outer peristome (the exostome) develops from the walls between the primary peristomial cells and the cells of the outer peristomial layer. It will be recalled that each primary peristomial cell subtends two cells of the outer peristomial layer. Here, as in the inner peristome, the first indication of secondary thickening is the migration of the cytoplasm and the nuclei toward the walls on which deposition will take place. Since in this case deposition takes place on both walls, the cytoplasm and nuclei in the primary peristomial cells move outward and in the outer peristomial layer they move inward (fig. 18). The deposit made by the primary peristomial cells is copious and, as observed by Lorch in *Mnium cuspidatum*, quite homogeneous in structure although somewhat stratified (fig. 19). This deposit is not confined to the tangential walls but extends considerably over the horizontal radial walls as seen in figure 13. The large size of the nuclei in this figure indicates incipient disintegration. The deposit on the outside of the outer peristome is of an entirely different structure from that on the inside, being distinctly spicular (fig. 19). The same types of deposit were also noted by Lorch in *Mnium cuspidatum.* A longitudinal section through a mature tooth

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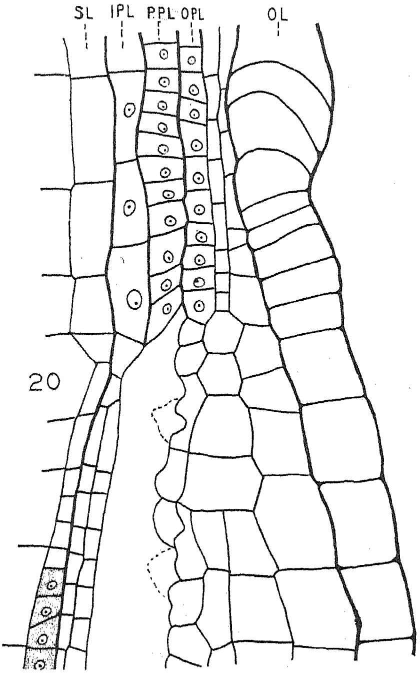
Explanation of figures 20–28

FIG. 20. Longitudinal section of a young capsule showing relation of peristomial layers to the outer regions of the capsule proper. FIG. 21. Longitudinal section of the basal region of the peristome. FIG. 22. Transverse section of the basal region of the peristome. FIG. 23. Transverse section of upper region of nearly mature peristome. FIG. 24. Outside view of portion of outer peristome. FIG. 25. Inside view of portion of outer peristome. FIGS. 26–27. Inner and outer views respectively of an outer peristome tooth. FIG. 28. Portion of inner peristome viewed from inside.



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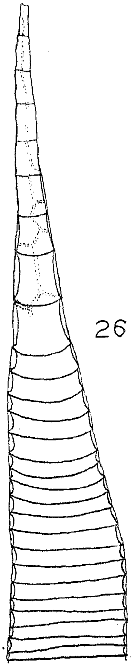

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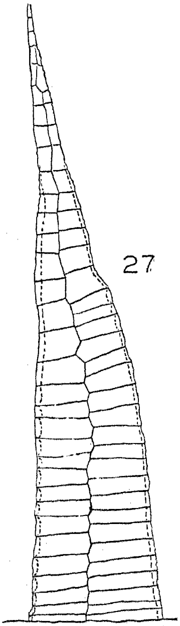

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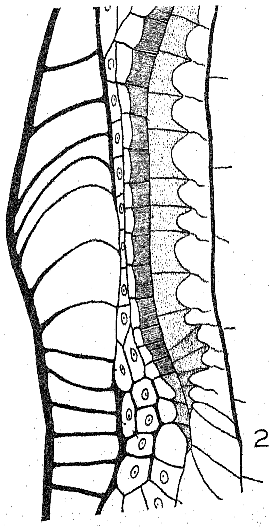

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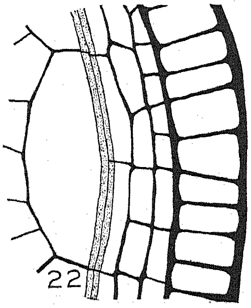

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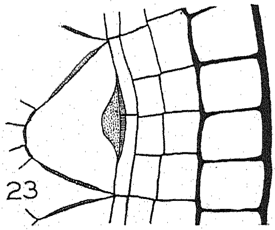

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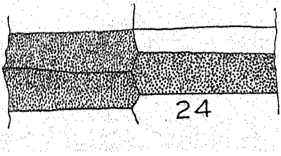

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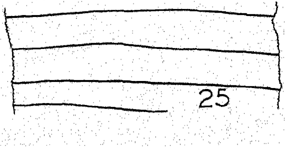

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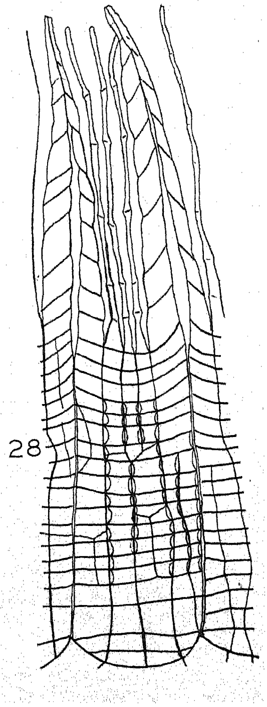

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is shown in figure 21. In *Ceratodon purpureus* Evans and Hooker found that the deposits on the two sides were essentially the same except that it was thicker and less uniform on the outside. In *Ceratodon* the early deposit is homogeneous but the later deposit is distinctly spicular on both sides. Since no deposition takes place at the junction of the vertical radial walls separating the primary peristomial cells and the walls of the outer peristome, except at the base, the peristome teeth separate at maturity.

As seen in figure 21 the peristome extends a considerable distance below the annulus. For a distance of about three cells from the base the deposit is the same on both sides, being homogeneous in structure. Between this portion and the cells of the operculum is a group of cells with somewhat thickened cell walls which apparently supports the peristome and acts as a hinge.

In the basal part of the outer peristome the deposit is continuous on both sides from tooth to tooth (fig. 22). This continuity of deposit decreases upward so that at the tip of the teeth it occupies only a narrow strip in the middle of the tangential cell walls (fig. 23). This condition contributes to the triangular shape of the teeth.

Since the form and markings of the peristome are of taxonomic importance it might be profitable to show their developmental relationship. Looking at the outside of a mature peristome tooth it will be seen that it is divided down the center by a somewhat zigzag line from which alternating lines extend out horizontally to the margins (figs. 24, 27). These lines represent the bases of the cell walls of the outer peristomial layer in which, it will be recalled, two cells subtend one cell in the primary peristomial layer. The margins show a narrow transparent strip due to the sparsity of secondary thickening along the edges. The inside view of a peristome tooth shows the absence of a vertical median line because this wall is only one cell wide. The horizontal lines represent, of course, the remnants of the horizontal radial walls (figs. 25, 26). In the upper portion, the outside median line may be visible because of the sparsity of secondary thickening in this portion.

The portion of the inner peristome which extends between two keels is subtended by one outer peristome tooth (fig. 28). Since the wall making up the outside of this portion of the inner peristome is the inner wall of a primary peristomial cell, the markings will correspond with those of the inside of the outer peristome tooth. However, owing to the lack of secondary thickening on this side, the cell outlines are very faint. The inside of the inner peristome shows from three to five vertical lines which represent the bases of the vertical radial cell walls. The horizontal lines represent the transverse radial walls. Occasionally extra lines appear which indicate irregularities in cell division.

DISCUSSION

In comparing the various accounts on peristome development, it is obvious that there are some differences of interpretation. These differences are concerned mainly with (1) the position of the inner peristomial layer with reference to the endothecium and (2) the relation of the peristome of a single peristomate moss to that of a double one.

Van der Wijk (1932, p. 34) in referring to Lantzius-Beninga's figure of *Hypnum silvaticum* (Tab. 65, Fig. 30) interprets the walls which develop into the inner peristome as the borderline between the endothecium and amphithecium. The similarity between the mature peristome of this species as shown by the above figure and *Aulacomnium heterostichum* would indicate that this is a misinterpretation. From all the accounts which have included the early stages of development, it is clear that the walls which form the inner peristome are between the first and the second cell layers *outside* of the endothecium.

Another interpretation somewhat similar to the above was made by Lorch in discussing *Mnium cuspidatum* (p. 249). He considers the position of the inner peristome as the outside limit of the columella. Since the outside limit of the columella in the region of the capsule is several cell layers within the cell layers which, projecting up into the region of the operculum, develop into the inner peristome, it is confusing to consider the limit of the columella as forming the inner peristome. Of course it is possible that his interpretation of the columella is different in the two regions.

In the account of the development of the peristome of *Ceratodon purpureus*, Evans and Hooker clearly show the relation between a single peristome and a double one. In all the cases investigated a single peristome develops from the walls between the innermost layer of cells of the amphithecium (IPL) and the next outer layer which in the present paper has been designated as the "primary peristomial layer" (PPL). Smith (1938, p. 101), however, in comparing the peristome of *Funaria* with that of *Ceratodon*, apparently misinterprets the position of the peristome of the latter, although his statement is not clear. He says: "Other genera, as *Ceratodon*, have a thickening of outer tangential walls only in the outer layer of the peristome."

To avoid confusion in interpretation it is suggested here that the same terminology be applied to the peristomial layers in both Haplolepideae and Diplolepideae. This is possible because from the evidence gathered from all accounts dealing with typical forms belonging to the Bryales, the peristomial layers are similar and have the same relative position in both the single- and double-peristomate forms. The principal variation is in the number of cells composing the layers, and in the number of cell-layers outside of the peristomial layers which, however, may vary to some extent at different levels of the operculum.

The conclusion of Philibert that a single peristome is homologous with the inner peristome of a double one seems to be true for the forms so far investigated if homology refers only to the primary cell walls. However, if our concept of homology includes the secondary thickening, which is after all the most important feature in peristome differentiation, his statement becomes only half true. According to Evans and Hooker both the inner and primary (the "outer") peristomial cell layers contribute to secondary thickening in a single peristome but in a double one, such as that of *Aulacomnium heterostichum*, only the inner peristomial layer contributes to the inner peristome.

The regularity of cell division and its significance in the development of the peristomial layers has been emphasized in this account as in all previous ones. That there is a striking regularity is undoubtedly true, but exceptions occur. Van der Wijk in his work on *Polytrichum* observed irregularities which even altered the number of teeth from the usual number of 64. In *Aulacomnium heterostichum* also some irregularities occur. As mentioned above, irregularities appear in the formation of the layers outside of the peristomial layers. The result is that the number of these layers varies to some extent vertically and the number of cells of which each is composed may not conform to the results expected from the fundamental square method. Even in the formation of the peristomial layers slight variations may occur. As is shown in figure 12 an anticlinal division may be occasionally duplicated in a corresponding cell of the next inner layer. Also anticlinal or periclinal divisions may take place out of turn centrifugally (fig. 15) but, so far as has been observed, the final result is always the same. In no instance has the number of peristome teeth been found to vary from the usual number of 16. In the inner peristomial layer, considerable variation takes place in all three planes. The most important of these variations concerns the number of vertical radial walls in the upper portion. The result is that the number of cilia varies from two to four. This fact is of some importance since they often enter into taxonomic considerations.

SUMMARY

1. The peristome of *Aulacomnium heterostichum* originates from the outer of the two fundamental layers in the opercular region of the sporophyte. This layer, which is called the amphithecium, is originally composed of eight cells.

2. By a regular alternation of periclinal and anticlinal cell divisions the amphithecium develops into six concentric layers, each of which has twice as many cells as the next inner layer. The number of cells in each layer is a multiple of four.

3. The double peristome is formed from the three innermost cell layers of the amphithecium.

4. Differentiation is initiated by the enlargement of the 16 cells of the middle of the three peristomial layers. Since the cells of this layer contribute more than those of the other layers to peristome formation and their number determines the number of peristome teeth, it is called the *primary peristome layer*.

5. The layer outside of the primary peristomial layer, which also contributes to peristome formation, is called the *outer peristomial layer*. Two cells of this layer subtend one cell of the primary peristomial layer.

6. The innermost layer contributes to the formation of the inner and is, therefore, called the *inner peristomial layer*. Since this layer is ultimately composed of from 64 to 72 cells, eight or nine cells of this layer subtend one cell of the primary.

7. The outer peristome is formed from a deposit of cell wall material laid down on the outer tangential cell walls of the primary peristomial layer contiguous to another deposit laid down on the inner tangential walls of the outer peristomial layer. The deposit on the inside is homogeneous while that on the outside is spicular.

8. The inner peristome is formed from the original inner tangential walls of the cells of the primary peristomial layer and the contiguous outer tangential walls of the inner layer. Only the cells of the inner peristomial layer contribute a deposit to the inner peristome.

9. The keeled condition of the segments of the inner peristome is due to the convexity of the inner walls of the primary peristomial layer.

10. Owing to the lack of deposit at the junction of the radial and tangential walls in the upper region of the inner peristomial layer, strips of cell plates separate to form from two to four cilia. This variation in the number of cilia is due to the variation in the number of cells in the inner peristomial layer subtending one cell in the primary.

11. The development of the peristome in *Aulacomnium heterostichum* is compared with the development of the peristome of other genera of mosses investigated.

12. The peristome of a single-peristomate moss develops in the same position with reference to the cell layers as the inner peristome of a double-peristomate moss.

13. It is suggested that to avoid misinterpretation the same terminology be applied to the peristomial layers in both the single- and double-peristomate mosses.

14. Some of the irregularities in peristome development are discussed.

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STUDIES ON THE EMBRYO OF HORDEUM SATIVUM—I. THE DEVELOPMENT OF THE EMBRYO

JAMES MERRY

(WITH FORTY-TWO FIGURES)

INTRODUCTION

Studies on the morphology of grass embryos have been based on observations either of embryos in early stages of development or of embryos and seedlings of mature seeds. In the first the gross morphological development was described and in the second the vascular anatomy of the embryo was given. The object of undertaking the work presented here was to describe the development of the embryo from the time of fertilization to the maturation of the ovule into a seed, and to give not only the development of the gross differentiation but that of the internal differentiation as well. To accomplish this a conventional histological study was made of the normal embryo at daily stages of development, and in addition the study of the vascular differentiation was aided by the use of the technique of growing excised embryos on an artificial medium.

When whole embryos are grown on an artificial medium small plants resembling seedlings are produced. The cells of the embryo which are potentially vascular tissue become more clearly differentiated in the cultured plant. Because of this vascular differentiation the cultured plants were found useful in studying the development of the normal embryo. The more developed the embryo is, the greater is the amount of internal differentiation in the plant grown from it. Thus the cultured plants show the potential differentiation which is not clearly visible in the normal embryos.

HISTORICAL SURVEY

It is proposed to give the historical origin of some of the terms commonly used in reference to grass embryos and to summarize the controversial views regarding grass embryo morphology for the benefit of those who may not be familiar with the extensive literature. For more detailed reviews of certain phases of embryo morphology the reader is referred to Van Tieghem (1872), Bruns (1892), Avery (1930), Randolph (1936), and McCall (1934).

According to Van Tieghem (1872) and others the earliest description of the embryo of grasses is that by Malphigi in 1687 of the embryos of *Avena* and *Triticum,* in which he recognized the structures now known as the scutellum, epiblast, and coleoptile. Gaertner has been credited with the first use of the term scutellum which is still commonly applied to the shield-shaped structure characteristic of the grass embryo. Richard in 1813, according-ing to Van Tieghem (1872), originated the term blast for that part of the embryo which becomes the stem of the plant, and from this he developed the term hypoblast for the scutellum. The small projection found on the outer face of some grass embryos was correspondingly called the epiblast, a term which is still in common use. The term blast itself has been displaced in English by plumule. Richard used the term cotyledon for the sheath around the blast, which Van Tieghem (1872) said was first given the present name, coleoptile, by Mirbel in 1815. The lower portion of the embryo has received less attention than the parts mentioned above, since there is little question about its homologies. The term radicle is used for that part of the embryo which becomes the primary root, and the surrounding tissue is called the coleorhiza. The term seminal roots has been used to include the radicle or primary root and any other roots present in the embryo. The argument over the homology of the scutellum has caused much difference of opinion as to what the region between the coleoptile and the scutellum actually is. In embryos such as those of *Avena* or *Zea* this region is of considerable extent. Van Tieghem (1872) considered that this was the node of the scutellum but later changed his views on the homologies of the embryo and called this region an internode (1897) between the scutellum as one leaf and the coleoptile as a second, as had Bruns in 1892. Čelakovský (1897) introduced the term mesocotyl for this part of the embryo because of his conclusion that the scutellum and the coleoptile together made up the cotyledon. The term mesocotyl has been commonly used, though the term "first internode" is now used by many workers who are interested in the growth of this part of the *Avena* seedling and who consider the scutellum and the coleoptile to be separate leaves.

The most debated points in the morphology of the grass embryo are the homologies of the scutellum, epiblast, and coleoptile, on which there seem to be three main views. The first considers the scutellum to be the first leaf, that is, the cotyledon of the embryo, and the coleoptile to be the first leaf of the plumule. The second view holds that the coleoptile is the cotyledon and that the scutellum is an outgrowth of the radicle or stem. The third view is that the scutellum and the coleoptile together make up the first leaf, that is, the cotyledon. A variation of the first view is that the scutellum is the first leaf, the epiblast the second leaf, and the coleoptile the third leaf of the plant. The papers already cited give a more complete development of these views.

The early studies on the formation and development of the embryo were based mostly on observation of whole embryos. Norner (1881) studied the early divisions of the zygote and proembryo of *Hordeum*, *Avena*, *Triticum*, and *Secale* by dissecting out whole embryos and mounting them in glycerine for observation. The oldest stages of which he gave figures were just beginning to show gross differentiation. He attempted to classify the arrangement of the cells according to the manner in which they divided, but the irregularity of the arrangement as shown by his figures would not seem to warrant this. Čelakovský (1897) showed five stages in the development of the upper part of the embryo to prove that the coleoptile is part of the scutellum. He did not identify the drawings by species, but stated that they were for the most part after Hanstein's figures.

Souèges (1924) traced the parts of the fully developed embryo of *Poa annua* back to the tiers of cells in the sixteen-celled proembryo. He also indicated that there was a definite arrangement of the cells and a regular sequence of cell divisions in the development from the fertilized egg. He maintained that the parts of the embryo are determined at least as early as the sixteen-celled stage. Randolph (1936) has given the only complete description of the development of a grass embryo in which the age of the various stages was determined. In the development of the embryo of *Zea* he found that there was no definite arrangement of the cells nor any regular sequence of divisions in the early stages.

MATERIAL AND METHODS

Hordeum sativum L. was chosen for this work because it is easy to grow in the greenhouse and a relatively large number of grains of the same age can be obtained from one head. Also, embryos of *Hordeum* varying as little as one day in age show recognizable morphological differences. A variety alpha, obtained from the College of Agriculture, Cornell University, was used for the work presented here. All the plants from which material was taken were grown in the greenhouse both in winter and summer.

The heads of the plants were examined several times a week and were tagged when the anthers had split. Two florets were fixed at this time and sectioned to determine when fertilization had occurred or would occur. At a selected time after tagging a head was picked and two or three ovules fixed for the study of normal development. All material was fixed in a solution of 50 per cent alcohol, 6 per cent formalin, and 6 per cent acetic acid. The normal embryos large enough to be removed from the ovules and plants cultured from the embryos were cleared and mounted in xylene in deep well slides and studied as temporary mounts. Camera lucida drawings were made from these mounts for record purposes. This material was of course taken into paraffin from the xylene. The rest of the material was run up to paraffin from the fixing solution by a short dioxane series. Sections 10 μ thick were made of the embedded material and stained in safranin and Delafield's haematoxylin. Measurements were made with an ocular micrometer both from temporary mounts and sections.

DESCRIPTION

In presenting the development of the embryo the various parts are treated separately except for the early stages or that phase of the development usually referred to as the proembryo. The differentiation of each structure, the manner in which it develops, and the differentiation of its vascular system are described. Also the vascular connection between the primary root and the rest of the embryo is traced.

Proembryo. Within the first two days after fertilization the first two divisions of the zygote occurred (figs. 1, 2, 3). The first was at right angles to the long axis of the ovule and the second occurred in the apical cell and was at right angles to the plane of the first division. After this three-celled stage the divisions seemed not to take place in any definite sequence or arrangement. By the third day the proembryo was made up of from 10 to 15 cells (fig. 4) and by the fourth of about 50 (fig. 5). The rate of division remained constant for several days, as determined by counting the number of cells in embryos of different ages. During the first seven days (figs. 1–8) no differentiation was observed except that the size of cells at the tip diminished and the cells divided more rapidly than those at the base. At the same time the proembryo became club shaped and tapered to a point at the base. About eight days after fertilization (fig. 9) the upper part of the embryo began to differentiate in outline so that the part which was to become the scutellum (fig. 9 *sc.*) was distinguishable. A swelling on the face of the embryo indicated the initiation of the stem meristem (fig. 9 *st.*), and above it the coleoptile began as a slight ridge (fig. 9 *c.*).

Scutellum. The portion of the eight-day-old embryo (fig. 9 *sc.*) which developed into the scutellum was 0.12 mm. long, 0.12 mm. wide, and 0.08 mm. thick; the measurement of the length being arbitrarily made on the basis of comparison with older embryos. The scutellum of the fully developed embryo (fig. 28 *sc.*) was 2.6 mm. long, 2.2 mm. wide, and 0.25 mm. thick. Consequently the developing scutellum grew somewhat more in length than in width, and the growth in thickness was slight in comparison to that in the other two dimensions. The fully developed scutellum was less than twice as many cells thick as the region from which it developed (figs. 36 and 42).

No definite meristem was observed in the scutellum, but most of the divisions seemed to occur in the layers towards the surface. The lower limit of the scutellum became clearly defined after about 13 days by an angle formed between the back of the scutellum and the lower side of the coleorhiza, which

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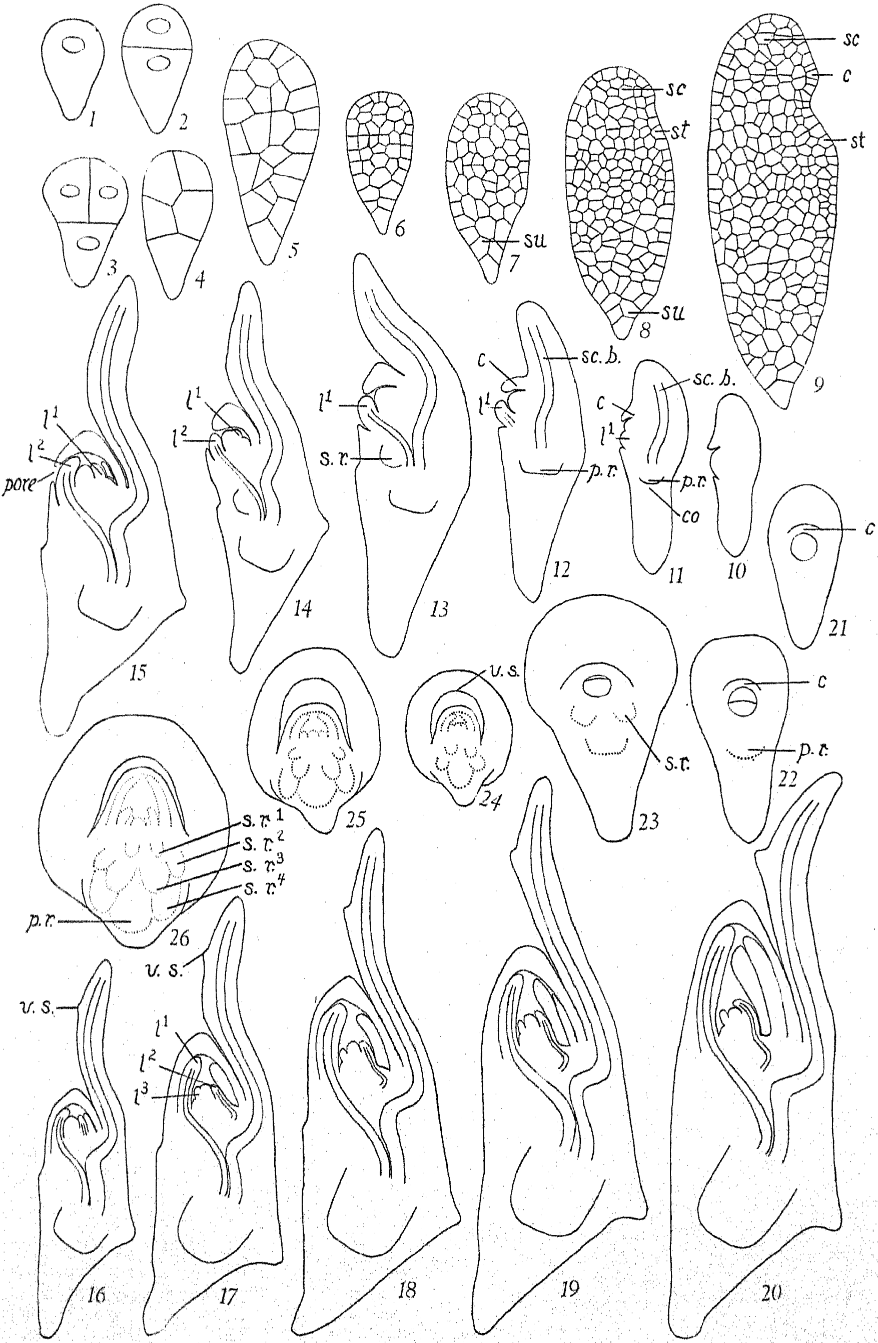
Explanation of figures 1–26

FIGS. 1–19. Longitudinal sections of embryos at daily stages from a fertilized egg to an embryo eighteen days old. 1–5 × 375. 6–9 × 165. 10–13 × 54. 14–15 × 40. 16–19 × 30. FIG. 20. Longitudinal section of an embryo twenty-one days old. × 30. FIGS. 21–26. Face views of whole embryos cleared in xylene; nine, ten, twelve, fifteen, seventeen, and twenty-eight days old respectively. 21–23 × 54. 24–26 × 17. *c*, coleoptile; *co*, coleorhiza; l^1, first leaf; l^2, second leaf; l^3, third leaf; *sc.* scutellum; *sc.b.*, scutellar bundle; *s.r.*, seminal root; *st*, stem meristem; *su*, suspensor; *v.s.*, ventral scale.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s. r^2
s. r^3
s. r^4
p. r.
25
24
v. s.
23
s. r.
22
c
p. r.
16
v. s.
17
v. s.
l^1
l^2
l^3
18
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20

became more acute as the development proceeded (figs. 12–14). The apex of the angle was coincident with the end of the endosperm which was undoubtedly the cause of this distinct boundary between the scutellum and the coleorhiza.

After 14 days periclinal divisions began to take place in certain cells in the ventral surface of the scutellum so that a ridge (figs. 16 and 24 *v.s.*) was produced which formed an arc from one side of the base of the coleoptile to the other side. This ridge finally extended about five cells above the surface and has been called the ventral scale by other authors.

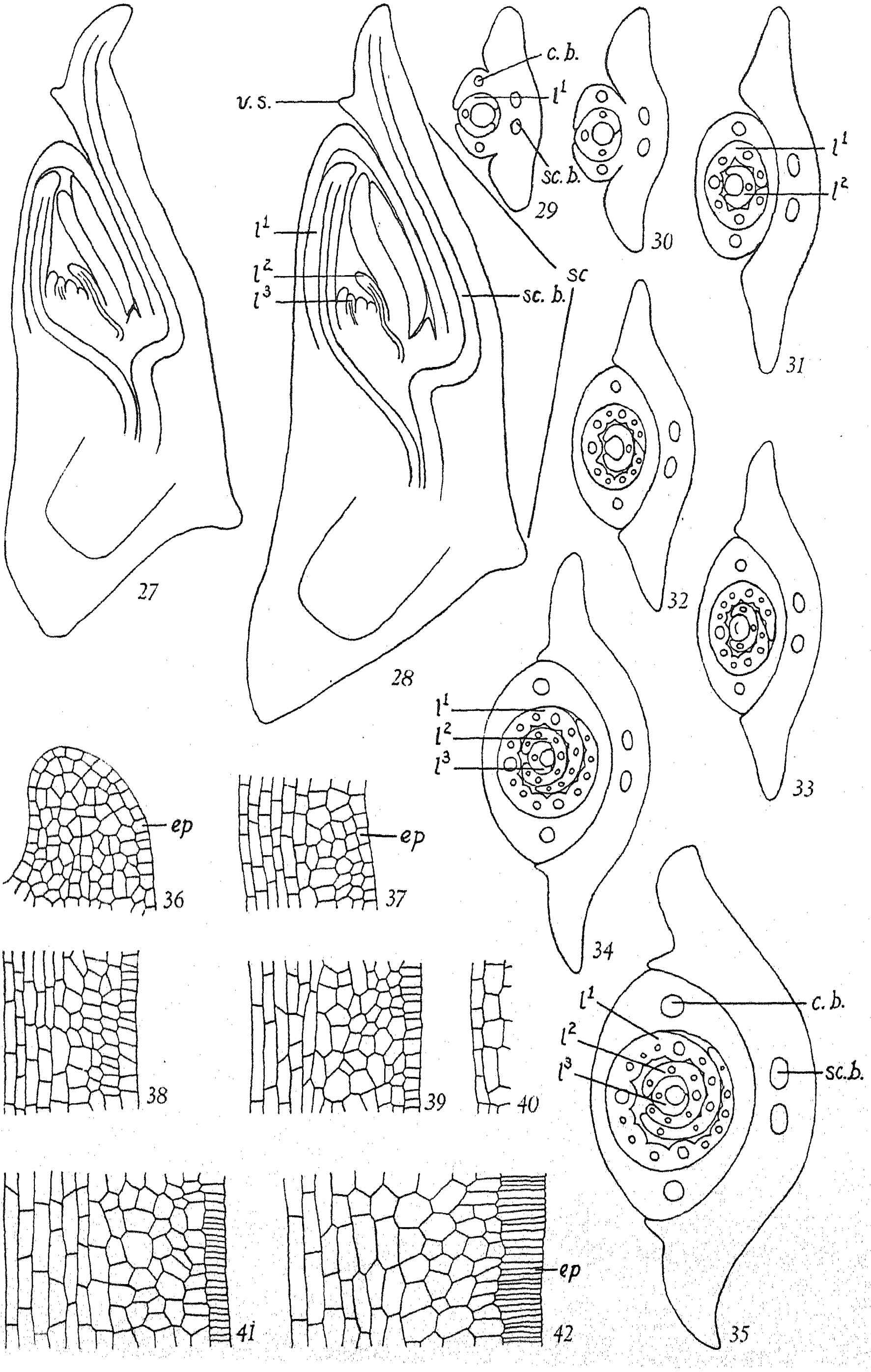
From 10 to 12 days after fertilization the epidermal cells on the dorsal surface of the scutellum, which is the surface in contact with the endosperm, appeared smaller than the internal cells or other epidermal cells (figs. 36 and 37 *ep.*). On about the 16th day these cells began to elongate in the dimension perpendicular to the surface and became recognizable as the epithelial layer (figs. 38, 39, 41 *ep.*). In the fully developed embryo these cells (fig. 42 *ep.*), in which the cytoplasm was more opaque than in the other cells, were three times as long as those of the same tissue on the 10th day (fig. 36 *ep.*) and were less than a third as wide.

The epidermal cells on the ventral surface of the scutellum within the ventral scale increased in length parallel to the long axis of the embryo so that they were several times as long as wide (figs. 41, 42). Similar epidermal cells outside the ventral scale were only slightly elongated (fig. 40).

The bundles of the scutellum were differentiated, ten days after fertilization, as two strands of elongated cells (figs. 11, 29, *sc.b.*). The lines in figure 11 are merely a diagrammatic outline of one bundle. These bundles formed an S-shaped curve on a level with the base of the stem meristem in the 11-day-old embryo (fig. 12 *sc.b.*) and the inflections became more pronounced as the embryo developed (figs. 12–20, 28 *sc.b.*). The bundles elongated with the growth in length of the scutellum and branched toward the outer edges. The branches turned back toward the base of the scutellum. The bundles increased in thickness throughout the development (figs. 29–35 *sc.b.*) by an

Explanation of figures 27–42

FIG. 27. Longitudinal section of an embryo twenty-eight days old. × 30. FIG. 28. Longitudinal section of the embryo of a mature grain soaked for twenty-four hours. × 30. FIGS. 29–34. Cross sections through the stem meristem of embryos twelve, thirteen, fifteen, sixteen, seventeen, and twenty-one days old respectively. 29–31 × 40. 32–34 × 30. FIG. 35. Cross section through the stem meristem of the embryo of a mature grain soaked for twenty-four hours. × 30. FIGS. 36–39, 41. Median longitudinal sections of a corresponding portion of the scutellum within the ventral scale of embryos ten, twelve, fifteen, eighteen, and twenty-one days old respectively. × 165. FIG. 40. Longitudinal section of the ventral surface of the scutellum outside the ventral scale of the embryo of a mature grain soaked for twenty-four hours. × 165. FIG. 42. Median longitudinal section within the ventral scale of the scutellum of the embryo of a mature grain soaked for twenty-four hours. × 165. *c.b.*, coleoptilar bundle; *ep*, epithelium; l^1, first leaf; l^2, second leaf; l^3, third leaf; *sc*, scutellum; *sc.b.*, scutellar bundle; *v.s.*, ventral scale.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l1
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sc
sc. b.
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c. b.
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42

increase in the number of cells. The phloem and xylem could not be distinguished in the bundles of the normal embryos, but from the cultured plants it was found that even in the bundles of 10-day-old embryos some of the cells were potentially xylem and some phloem. Also from these plants it was determined that the bundles were collateral, with the xylem on the ventral side, as has been reported for other grass embryos.

Coleoptile. The coleoptile was formed from the general region of the proembryo which also gives rise to the scutellum (fig. 9 *c.*) and first appeared as a crescent-shaped ridge above the stem meristem (fig. 21 *c.*). This ridge was extended downward until it encircled the growing point and then grew out from the rest of the embryo as a sheathing tube. The sides of the tube gradually approach each other so as to leave a narrow vertical slit or pore, through which the shoot emerges during germination. The side next to the scutellum grew faster than the other side so that the pore became located on the front side of the coleoptile (fig. 15 pore). In the later stages the ratio of the number of cells above and below the pore remained about the same.

The bundles began to differentiate on about the 11th day opposite each other on the sides of the coleoptile (fig. 29 *c.b.*). The size of the bundles increased throughout the development of the embryo by an increase in the number of cells (figs. 29–35 *c.b.*). From the cultured plants it was determined that these bundles were collateral with the xylem on the side toward the center of the coleoptile.

Stem Meristem. By going back through the stages of the developing embryo the region which was to become the stem meristem was recognized seven or eight days after fertilization (figs. 8, 9 *st.*). It began as a swelling on the face of the embryo due to the higher frequency of cell divisions in that part. The cells were smaller than those of the surrounding part of the embryo (fig. 9 *st.*). The size of the meristem was constant throughout the development of the embryo, though there was some variation at different points in each plastochron.

On the 10th day the first leaf primordium was initiated (fig. 11 l^1), and the midvein of the first leaf began to differentiate on about the 12th day (fig. 29 l^1). In the embryo of the mature grain there were nine pairs of lateral bundles in the first leaf (fig. 35 l^1). Counting from the midvein, pair four was differentiated on the 13th day (fig. 30), pairs two and seven on the 15th day (fig. 31 l^1), pairs three and five on the 16th day (fig. 32), pair one on the 17th day (fig. 33), and pairs six, eight, and nine on the 21st day (fig. 34 l^1).

The primordium of the second leaf was first observed in the 13-day-old embryo (fig. 14 l^2). Its midvein began to differentiate on the 15th day (fig. 31 l^2). There were three pairs of lateral bundles in the second leaf of the fully developed embyro (fig. 35 l^2). Pair 2 began to differentiate in the 17-day-old embryo (fig. 33), and pairs 1 and 3 in the 21-day-old embryo (fig. 34 l^2).

The primordium of the third leaf appeared on about the 16th day (fig. 17 l^3). The midvein of this leaf differentiated on the 21st day (fig. 34 l^3), and no other bundles were formed in the third leaf in the normal development of the embryo (fig. 35 l^3).

Root System. The primary root primordium began to develop about 10 days after fertilization (figs. 11, 22 *p.r.*). In the cultured plants the primary root had eight strands of protoxylem alternating with eight strands of phloem as did the other roots formed in the embryo. The number of cells in each strand increased with the age of the embryo, and the cortex of the roots also increased in thickness. The first pair of seminal roots began to differentiate on the 12th day (figs. 13, 23 *s.r.*). The second pair began on the 15th day above and between the first pair (fig. 24). The third pair was formed outside and above the second pair on the 17th or 18th day (fig. 25). A fourth pair of primordia was formed after 21 days between and slightly above the third pair (fig. 26 *s.r.*). All of these primordia were formed in front of the primary root.

Coleorhiza. The coleorhiza was differentiated from the lower part of the 10-day-old embryo (fig. 11 *co.*) by the development of the primary root primordium. The other root primordia grew down within the coleorhiza and were often separated from each other by thin layers of the tissue of the coleorhiza. The coleorhiza grew partly by cell elongation but mostly by scattered cell divisions. No vascular bundles were formed in this part of the embryo.

Suspensor. The cells near the base of the proembryo were larger than those in the other parts (figs. 7 and 8 *su.*) and stopped dividing after about 10 days. They formed the suspensor, which was not more than 0.1 mm. long and which in the fully developed embryo was no longer recognizable.

Transition Region of the Primary Root. The metaxylem of the primary root was connected to the midvein and the second, fourth, and seventh pairs of lateral bundles of the first leaf. The protoxylem and a little of the metaxylem were connected to the scutellar bundles.

Part of the phloem strands of the primary root passed into the center of the transition region and formed a large mass of phloem. This mass was observed to divide into two parts higher up in the region. One portion was traced to the midvein of the first leaf and the rest to the phloem of the fourth and seventh lateral bundles of the first leaf and to the scutellar bundles. The remainder of the phloem of the primary root was connected to the second pair of lateral bundles and to the scutellar bundles.

Vascular Relationships. The two bundles of the scutellum were connected with the primary root as it began to develop on the 10th day. The two bundles of the coleoptile began to differentiate on the 12th day and soon became connected with the bundles of the scutellum. At the base of the coleoptile the bundles from it turned at right angles and passed back around the other bundles, and joined the scutellar bundles where the latter made the second bend to pass down to the transition region.

The midvein of the first leaf passed alone through the transition region to the primary root, though the second pair of lateral bundles of the first leaf came very close to it as they were differentiated in the same region. The fourth and seventh pairs of lateral bundles of the first leaf were so close together in the transition region that they practically constituted a single pair of bundles. The connections of the other bundles of the stem were not differentiated in the normal embryos, but in the cultured plants the bundles turned at right angles above the transition region of the primary root and entered the transition regions of the other seminal roots. These latter regions were so close together that they formed a very complicated plate in the front of the embryo.

DISCUSSION

Since the cell walls formed by the first two divisions of the zygote were observed to be at right angles to each other, whereas Norner (1881) and Souèges (1924) found them to be parallel, and since the subsequent divisions are even more irregular, it would seem that no special significance can be attached to the sequence of cell divisions nor to the arrangement of the cells in the development of the embryo. This is in agreement with the findings of Randolph (1936) and may be interpreted as an indication that the factors controlling the growth of the embryo affect the embryo as a whole rather than definite individual cells. Souèges' (1924) stated that the parts of the embryo are already determined in particular cells in the 16-celled embryo.

The smaller size and greater number of cells in the upper part of the proembryo after about four days suggest a gradient from the apex to the base of some factors which control the rate of division of the cells. The appearance of smaller cells and more division figures in certain parts of the embryo on about the seventh day seems to indicate that similar factors had become concentrated in those regions.

In the developing scutellum the cells are larger than elsewhere and the divisions are scattered, so that there seems to be no localization of such factors in that part.

In the development of the embryo the region which is to become the scutellum can be distinguished from that part which becomes the stem meristem. The coleoptile develops from the same region as that which gives rise to the scutellum. Because of this the scutellum and the coleoptile are considered to be closely associated parts distinct from the stem. There are other indications of this distinction which, while they cannot be offered as proof, add to the support of the conclusion based on the development of the embryo. These are as follows.

The bundles of the scutellum develop before the bundles of the stem and are connected directly with the primary root. However this does not prove that the scutellum is morphologically distinct from the stem, since the midvein of the first leaf also is connected directly with the primary root and has no connections with any of the other bundles of the stem.

The connection of the coleoptilar bundles with the scutellar bundles indicates a closer relationship between the coleoptile and the scutellum than between either of them and the stem. In *Hordeum* the coleoptile and scutellum are similar in possessing two bundles in contrast to the one main bundle of the foliage leaves. The scutella of some of the wild species of *Hordeum* and of other grasses have only one bundle, and whether one bundle or two is the primitive condition is difficult to determine. In the corresponding structure of the embryos of other monocotyledons, which are usually considered to be less specialized than grass embryos, there are usually two and sometimes four bundles (Taylor 1921).

The scutellum and coleoptile are different in appearance and function from the foliage leaves, but this point should not be stressed, since foliage leaves are known to be greatly modified. While these additional indications of the separation in question cannot be defended as proof, it is equally difficult to find any conclusive evidence that the two structures are modified foliage leaves. It seems possible to consider them merely structures peculiar to the embryo.

The scutellum alone or the scutellum and the coleoptile together have been generally considered as the cotyledon of the embryo. The term cotyledon, according to the Oxford English Dictionary, ''was first used in the botanical sense by Linnaeus as referring to those seed leaves which are not in themselves depositories of nutriment but act as organs of absorption, in which he saw an analogy to the function of the cotyledon in the zoological sense.'' The term had been previously applied to the lobes on certain mammalian placentae. If such a meaning is to be preserved, then the scutellum of grass embryos is more rightfully called a cotyledon than any other structure of the embryo of any other plant, since with the development of the epithelial layer it is certainly the structure most specialized for absorption. From the standpoint of development it is concluded that the scutellum is homologous with the cotyledon of other monocotyledonous embryos.

The various views of the homologies of the parts of the grass embryo have caused much confusion on the terminology of that part of the axis between the node of the first foliage leaf and the primary root. In *Hordeum* as in other grasses this region is very complex. The lower portion is covered by the coleorhiza on the outer face and by the scutellum on the inner face. Just above the primary root is the transition region from it to seven of the bundles of the first leaf and to the scutellar bundles. Above this are the four pairs of seminal roots and the transition regions through which the bundles of the stem are connected with them. The coleoptilar bundles are present in this region from the divergence of the coleoptile to the point where they connect with the scutellar bundles.

Van Tieghem (1872), Avery (1930), Boyd and Avery (1936), and others have shown that this region varies in different species of grasses; it does not, therefore, seem possible to find a natural term which will fit them all. Van Tieghem (1872) divided the grass embryos he studied into three groups on the basis of the morphology of the region. In the members of the first group the coleoptile is inserted just above the scutellum, as in *Hordeum* and *Triticum*. In those of the second group the coleoptile is inserted some distance above the scutellum and the region is traversed by a "cortical" bundle, as in *Avena* and *Zizania*. In plants of the third group the coleoptile is inserted some distance above the scutellum and the region between is not traversed by a cortical bundle, as in the embryo of *Zea*.

Avery (1930) described the anatomy of the seedlings of *Triticum*, *Avena*, and *Zea*, showing the differences between the three groups of Van Tieghem's classification. The cortical bundle of the second, or *Avena*, type is the scutellar bundle which extends almost to the divergence of the coleoptile where the coleoptilar bundles connect with it. From this point according to Avery (1930) a "common bundle" passes down to the primary root. Avery (1930) and Boyd and Avery (1936) regarded the scutellar bundle as extending only to the point where it met the coleoptilar bundles. However, in the ten-day embryo of *Hordeum* two bundles connect the scutellum with the primary root meristem and no coleoptilar bundles are present. In this case it is not possible to distinguish the "scutellar trace" from the "common bundle" as described by Boyd and Avery (1936). From the development of the embryo in *Zizania*, an embryo of the *Avena* type, as illustrated by LaRue and Avery (1938) it also appears that the "common bundle" cannot be distinguished from the "scutellar trace" at an early age. In the *Zea* embryo as described by Avery (1930) the scutellar bundle does not extend up into the region between the scutellum and the coleoptile. According to Avery (1930) the coleoptilar bundles diverge from two bundles in the stele. It seems more consistent with the condition in other embryos to consider that the coleoptilar bundles extend down through the region in question and connect with the scutellar bundles. In the *Hordeum* embryo there is no elongation of the axis between the scutellum and the divergence of the coleoptile, and the coleoptilar bundles are clearly connected with the scutellar bundles.

It is suggested that in the second, or *Avena*, type of embryo the "meristematic region" described by Avery (1930) is in a part of the scutellum, and that the region of the axis between the level of divergence of the scutellum and the coleoptile is the transition region between the stem and the primary root surrounded by an elongated portion of the scutellum. In the third, or *Zea*, type the absence of a cortical bundle in the region between the scutellum and the divergence of the coleoptile is due to the fact that the "meristematic region" as shown by Avery (1930) is above the scutellar bundle. The bundles from the coleoptile extend through this region to connect with the scutellar bundle, and so it is considered that in this type of embryo the region between the divergence of the scutellum and that of the coleoptile is part of the transition region between the primary root and the stem, surrounded by and fused with an elongated portion of the coleoptile.

As has been pointed out, it does not seem possible to find one natural term which will accurately describe the condition in all the types of grass embryos. It is the writer's belief that the terms which have been applied to this region are not strictly correct, but developing a new artificial term would only add to the confusion.

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SUMMARY

1. The normal development of the embryo of *Hordeum sativum* is described, and the development of the vascular system of the embryo is interpreted from plants grown in culture from embryos of different ages.

2. The proembryo develops with no definite arrangement or sequence of cell divisions.

3. The scutellum and stem meristem begin to differentiate at eight days after fertilization.

4. The coleoptile is formed from the region which becomes the scutellum and is closely associated with the scutellum.

5. The scutellum and the coleoptile are considered to be structures morphologically distinct from the foliage leaves and peculiar to the embryo.

6. The time of differentiation of the leaf primordia, the bundles of the leaves, and the seminal root primordia is given.

7. The vascular relationships of the various parts of the embryo are described.

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EXPERIMENTS ON THE INHERITANCE OF THE "PLUS" AND "MINUS" CHARACTERS IN GLOMERELLA CINGULATA

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(WITH ONE FIGURE)

INTRODUCTION

Edgerton (1914) reported the occurrence of two distinct types of cultures in one or more species of *Glomerella* isolated from various hosts. These types he designated as "plus" and "minus," regarding them as "sexual strains." Although the species of fungi concerned were not definitely identified, it appears probable that at least the one isolated from cottonwood and used extensively in Edgerton's work was *Glomerella cingulata* (Stonem.) S. and v. S. Monoascosporic lines of either the "plus" or the "minus" type were capable of producing fertile perithecia in vitro, though most perithecia of minus lines failed to develop mature spores. When a "plus" isolate was grown in plate culture with a "minus" isolate from the same host, fertile perithecia developed in great abundance along a line where the two strains met. Asci containing the full complement of spores were isolated from perithecia produced along the line between the isolates and cultured individually without separating the ascospores. It was found that both the "plus" and "minus" strains were commonly, though not always, produced in the same ascus. This and other evidence led Edgerton to take the view that fertilization occurred when the two strains came together in a plate (cf. Shear and Wood 1913). He pointed out, however, that the process of fertilization had not been fully studied and that it was impossible to explain with certainty the phenomena he had described.

Though more than 25 years have elapsed since Edgerton's valuable pioneer contribution, and great advances have been made in the field of genetics of fungi, it is still uncertain whether genetic combinations occur between the "plus" and "minus" strains of *G. cingulata*.

In working with a culture of *G. cingulata* from rotted apple, the writer obtained monoascosporic isolates that seem to correspond to Edgerton's plus and minus types. In December, 1939, when the eight spores of an ascus were

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cultured separately, it was observed that four lines were of the "plus" type and four "minus." Experiments were then initiated to study comparatively in pedigreed cultures the incidence of "plus" and "minus" lines in asci arising in monoascosporic "plus" and "minus" clones, respectively, and in asci obtained from perithecia on the line between "plus" and "minus" isolates. This work was unavoidably interrupted in March, 1941, when the writer was called into military service. Though it is hoped that the investigation may be resumed later, it seems more advisable to give the following brief report of the available results than to await the possibility of making a more complete report after further investigation.

MATERIALS AND METHODS

The original culture on which the greater part of the present work has been based was obtained from a bitter rot lesion on a Black Ben Davis apple from Tennessee. Reinoculations into apples incited the characteristic rot in all cases. Another culture that was used to a very limited extent was obtained from Miss A. J. Watson, who had isolated it from a specimen of *Celastrus scandens* L. secured in New Hampshire. The two races represented were designated southern and northern respectively.

Various media were used to culture the fungus. It was found that potato dextrose agar served quite well for the production of conidia and ascospores, and this was selected as the standard medium for the work. The agar was unwashed and the commonly used formula was employed. Varying the pH and the relative carbon content, within limits, affected the rate of growth of the fungus but not the production of either ascospores or conidia. Oat agar, sometimes recommended for use in the production of perithecia, gave no apparent increase in this case. Monosporic isolations were made by means of glass needles used with a stereoscopic binocular microscope. In most cases the spores were removed without regard to their relative position in the ascus.

TYPES OF ISOLATES OBTAINED

Two general types of cultures, designated as light and dark,[1] were obtained. The color differentiation was definite in all cultures and together with other characteristics readily served to distinguish the two types.

The light type is characterized by an abundance of light-colored aerial mycelium. Conidia are produced sparingly but occasionally acervuli are formed which produce pink spore-masses. In the course of a few days cultures of this type produce perithecia which contain fully developed normal asci with viable ascospores. These perithecia are in groups and do not occur distributed throughout the culture like those of the dark type.

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[1] Since it is not definitely known whether these types actually enter into genetic combinations with each other, they are hereinafter designed as light and dark. They seem to correspond, respectively, to Edgerton's (1914) "plus" and "minus" strains.

The dark type produces very little aerial mycelium, and in the course of a few days appears carbonaceous. It always produces abundant conidia in large masses on the various media employed, the masses of spores at first giving the cultures a salmon-pink surface coloration. Later perithecia are produced in large numbers over the surface and submerged throughout the medium. These perithecia, however, seldom form asci and when asci are produced they are usually abnormal, the spores not germinating readily. It was found that only one in several hundred perithecia formed even imperfect asci.

When the two types are grown together in the same Petri dish there is a distinct line of perithecia at the junction of the colonies. These contain normal asci with the usual complement of ascospores.

DERIVATION AND BEHAVIOR OF CLONES OF THE SOUTHERN RACE

As explained above, the original culture, designated as stock culture No. 1, was isolated from an apple. Two single ascospores picked out at random from this culture yielded the clones from which all the others of this group were derived. One, a dark type, was designated as 1C and the other, a light types, as 1A. These isolates were then grown together in the same dish, and from the line of perithecia that developed where the two met, single asci were picked out and the spores isolated. One set of eight cultures, X2, derived from the ascospores of a single ascus, was retained for further study, all subsequent cultures being derived from this set.

The derivation and types of the clones of the southern race are diagrammatically shown in figure 1. A solid black disk designates a dark type clone, whereas a circle designates a light type. While the ascospores were always isolated in full sets of eight, occasionally some spores failed to germinate; this accounts for the blank spaces where sets of cultures derived from certain asci are represented. Although the dark type strains are designated first, followed by the light in indicating a set, this does not refer to their relative position in the ascus. Sets marked by the letter X were obtained from the line of perithecia developed between two opposite types, whereas those without the X were obtained from clones grown separately.

Unbroken lines trace the descent of isolates from a monoascosporic clone, and grouped columns of sets below the end of such lines are from the same colony. Broken lines show the derivation of sets from perithecia taken from the line between the dark and light isolates. For example, sets X30 to X38 were obtained from the line of perithecia formed by pairing 58(4) and 58(7). Sets grouped by brackets are all from the same perithecium. For example, sets 91 to 100 were from a single perithecium taken from culture 57(5).

The light and dark strains of the southern race were distinctly differentiated in culture, even under widely varied environmental conditions.

Both types remained constant, whether propagated by conidia or mycelium. It is concluded that these types are hereditary rather than modifications induced as responses to environment.

With one exception asci from monosporic clones of the light type yielded either all dark cultures or four dark and four light. In the exceptional case there were taken from a perithecium of clon 58(7) three asci yielding all light cultures and five asci that gave all dark cultures. When several asci were

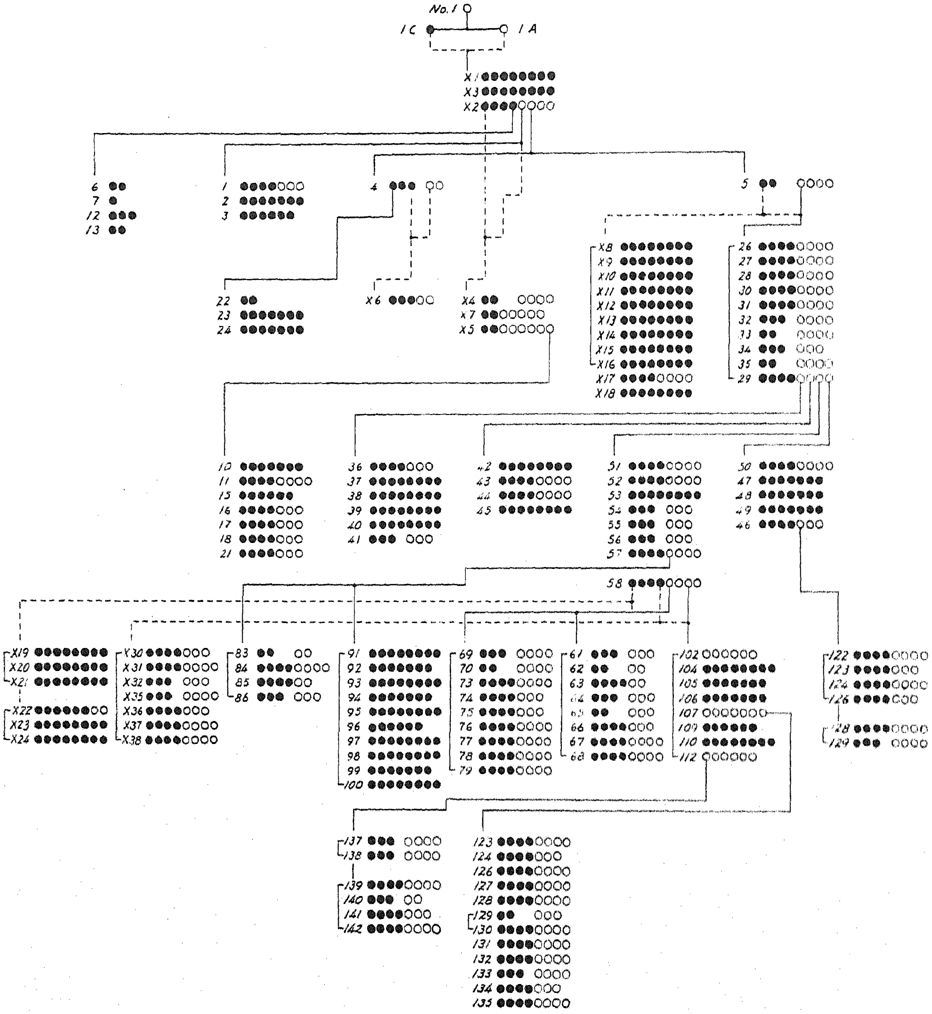

FIG. 1. Derivation and type of the clones of the southern race of *Glomerella cingulata* (see text).

taken from a single perithecium they yielded either all dark cultures, or half dark and half light, with the one exception mentioned. In this exceptional case, however, when certain clones from asci that had given all light cultures were studied, for example 107(7) and 112(1), they gave rise to asci yielding dark as well as light strains.

Asci obtained from the dark strain grown alone yielded only dark cultures. The number of isolations is certainly relatively small, because most of the ascospores did not germinate, but as far as the experiment was carried the dark colonies produced nothing but dark offspring.

When asci were taken from perithecia at the junction of dark and light colonies there usually were produced either all dark sets or sets consisting of half dark clones and half light. There were certain instances, however, in which the ratio of the two types in a set was not 1:1, for example: X5 and X7 in which there were 2 dark and the remainder light, and X22 in which there were 6 dark and 2 light. Here again all sets from the same perithecium were alike except X22.

REACTION BETWEEN ISOLATES

Southern race. To determine whether all dark isolates of a set would react to form lines of perithecia when in contact with each light isolate of a set, the clones of certain sets were paired in all possible combinations. When, for instance, the clones of set X2 were so paired it was found that there was a definite line of perithecia where each dark isolate came in contact with each light isolate, but where light isolates came together there was never any such line of perithecia formed, the colonies merely merging. The dark colonies likewise placed together showed no indication of any reaction with one another. In the sets in which there were all light or all dark clones from a single ascus, as for example, 107 and 110, it was found that there were lines of perithecia only between dark and light isolates when the clones of the two sets were placed in all possible combinations.

Northern race. With this culture the clones derived from a single ascus were either all of the dark type or all of the light type. The number examined was small, only 15 asci in all; but this seems to be the normal situation in this race in contrast to that found in the southern race. In pairing the dark and light strains of the northern race, it was found that a line of perithecia was formed only when dark met with light.

Southern race with northern. A southern light strain paired with a northern dark gave a line of perithecia at the junction, and a northern light paired with a southern dark likewise gave perithecia at the meeting line. Southern dark and northern dark gave no line of perithecia, nor did southern light and northern light.

SUMMARY AND CONCLUSIONS

A race of *Glomerella cingulata* (Stonem.) S. and v. S. obtained from a rotted apple from Tennessee was studied for inheritance of light and dark strain characters (apparently corresponding, respectively, to "plus" and "minus" of Edgerton).

Monoascosporic colonies were always either light or dark.

A comparative study was made, using pedigreed cultures, of the incidence of light and dark lines in asci taken, respectively, from monoascosporic light clones, monoascosporic dark clones, and the line of perithecia developed where light and dark strains met in plate culture. Monoascosporic light clones gave asci that yielded all dark clones or half dark and half light, with the exception of one perithecium in which the asci yielded all dark or all light. Monoascosporic dark clones gave asci that yielded only dark clones. Asci taken from perithecia produced where the light and dark types met usually yielded all dark clones or half dark clones and half light. Several such asci, however, yielded dark and light clones in 3 : 1 or 1 : 3 ratio.

In limited experiments with a northern race of the same fungus somewhat different results were obtained.

Perhaps the most noteworthy aspect of the results here reported is the common production of all dark clones or half dark clones and half light from asci originating in monoascosporic light lines of the southern race. Explanation of this remarkable phenomenon of continuous production of dark and light clones in 1 : 1 or 1 : 0 ratios from asci of a homothallic haploid line must await the results of further work.

The work was carried on under the direct supervision of Dr. G. W. Keitt, to whom the writer is greatly indebted for suggestions and for help in preparing the manuscript.

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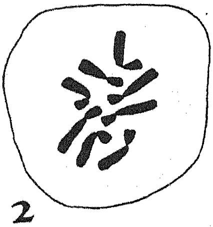
CYTOPHYLETIC ANALYSIS OF ASTRANTHIUM INTEGRIFOLIUM

J. T. BALDWIN, JR.

(WITH FOUR FIGURES)

Astranthium integrifolium (Michx.) Nutt., the western daisy, is more generally known as *Bellis integrifolia* and is then congeneric with the English daisy. According to the manuals, the plant occurs from Kentucky and southwestern Missouri to Texas and blooms from May to July.

Seed of *A. integrifolium* (*Mary Wharton 4329,* University of Michigan Herbarium; near Liberty, Casey County, Kentucky) planted in the University of Michigan Botanical Gardens in January 1940 produced flowering specimens during November 1940 and several subsequent months. One of the plants, drawn by Eduardo Salgado, is shown in figure 1; the



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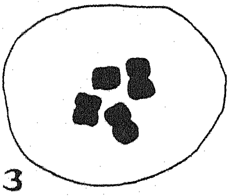

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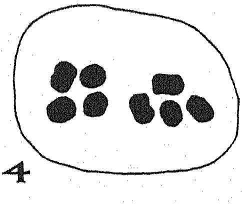

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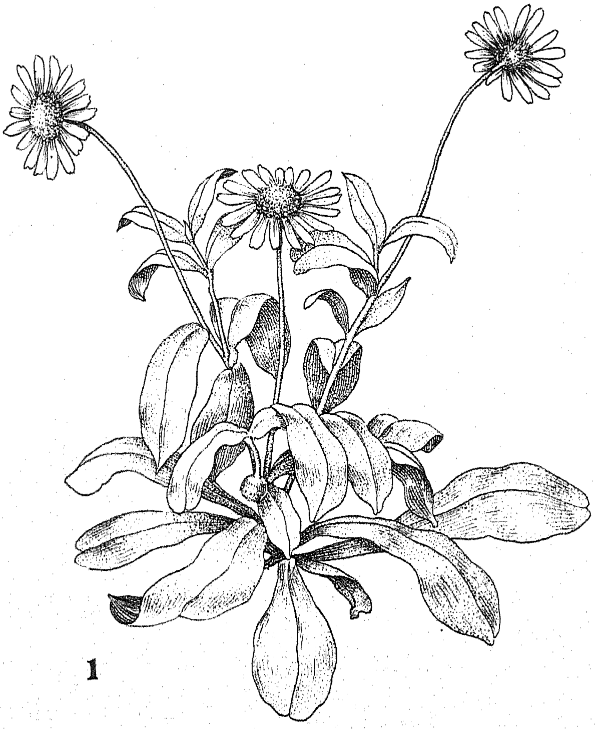

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FIG. 1. *Astranthium integrifolium* beginning to flower. × 0.7. FIGS. 2–4. Chromosomes of *Astranthium integrifolium*: $2n = 8$ at metaphase in leaf cell; $n = 4$ at first and second metaphase in pollen mother-cell. × 1400.

basal leaves are still present, and the flowers are maturing. The chromosomes were investigated in aceto-carmine smears of leaves, roots, and anthers: $2n = 8$ (fig. 2), $n = 4$ (figs. 3, 4). This somatic number was also determined for plants sent by Miss Wharton from Big Hill, Madison County, Kentucky, and for plants collected with the aid of H. T. Shacklette and A. M. Harvill of the University of Kentucky from near Nashville, Davidson County, Tennessee, from Cliffton, Woodford County, Kentucky, and from the University of Kentucky Botanic Garden. Meiosis was in process in the Tennessee plants on April 15, 1941: $n = 4$.

Representatives of this species are recommended for use in classes in microtechnique. Mitosis may be readily studied in easily made leaf smears (for method, see Baldwin 1939; Sen 1940); meiotic material is not difficult to get, for the flowers of a head develop differentially over an extended period. The plants normally die after blooming, but, if the stems are cut back, flower production will be prevented and thus a constant supply of young leaves insured.

Negodi (1936), working with plants grown from seed obtained from a European botanic garden and identified by De Candolle's (1826) description, reported *Bellis integrifolia* Michx. to have an n-number of 9 chromosomes; in view of the present study of material from the wild, one judges that Negodi mistook the species. Chromosome numbers have been determined for five other representatives of *Bellis:*

	n-number	$2n$-number	Authority
B. annua L.	9		Negodi 1937a
B. perennis L.	9		Ishikawa 1911
			Winge 1917
			Negodi 1937a
		18	Heitz 1926
B. rotundifolia Boiss. & Reut.	9		Negodi 1937b
B. mexicana A. Gray	18		Negodi 1937b
B. sylvestris Cyrill.	18		Negodi 1937a
		54	Tischler 1936

Steyermark (1940) recognized the validity of Nuttall's monotypic *Astranthium.* Chromosome numbers give an additional basis for this generic separation: *A. integrifolium* has an n-number of 4; the six investigated *Bellis* species, n-numbers of 9, 18, or 27. Perhaps *Bellis* (the genus, as listed in *Index Kewensis,* includes about forty species, approximately a third of them being native to the new world) is an amphidiploid result of a union between a 4-chromosome system, of which *Astranthium* is an expression, and a 5-chromosome system. In this connection, it would be interesting to know the chromosomal situation in *Eclipta* L., for Nuttall (1841), writing of *Astranthium,* said: "This genus appears to be much more allied by the fruit to *Eclipta* than to *Bellis.*"

SUMMARY

Astranthium integrifolium has an n-number of 4 chromosomes, a $2n$-number of 8; *Bellis*, as investigated by other workers, has a basic number of 9: these chromosomal data support the separation of *Astranthium* from *Bellis*.

A. integrifolium is recommended for use by students in microtechnique.

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STRUCTURAL FEATURES OF THE SHOOT APICES OF DIPLOID AND COLCHICINE-INDUCED, TETRAPLOID STRAINS OF VINCA ROSEA L.[1]

G. L. Cross and T. J. Johnson

(WITH TWENTY-FOUR FIGURES)

INTRODUCTION

Vinca rosea (Madagascar periwinkle) is an ornamental plant of considerable importance in the southwestern states (fig. 1). Because of its resistance to drouth and disease, and because it blooms over a relatively long period of time during the summer months, the plant is used extensively in public and private gardens. In an effort to produce new and improved varieties through the induction of polyploidy (Eigsti 1938), Schnell (1940) treated seeds and seedlings of both the red and white varieties of *V. rosea* with various mixtures of colchicine, prepared in water, mineral oil, and lanolin. An assortment of tetraploid and octoploid plants, including a few chimeras, was obtained from this treatment. One especially promising white tetraploid strain appeared, and it is being cultivated experimentally at the

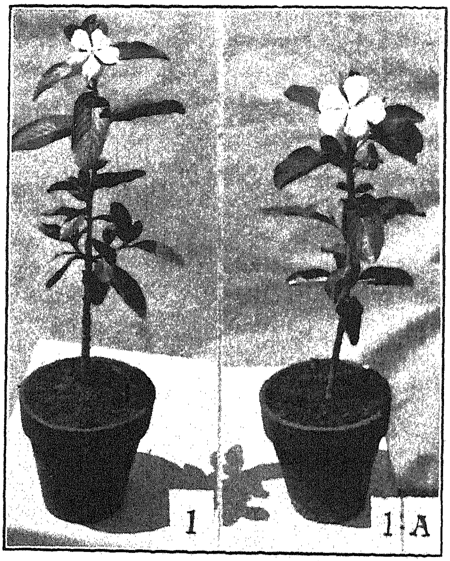

Fig. 1. Diploid plant. Fig. 1A. Tetraploid plant. Note shorter, thicker main axis and heavier, darker leaves. × ⅛.

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[1] Contribution from the Botanical Laboratory of the University of Oklahoma, n.s. 66. Publication of the figures was assisted by the Lucien M. Underwood Memorial Fund.

University of Oklahoma. The plants of this new strain have somewhat more massive stems, thicker and greener leaves, and larger flowers (fig. 1A). They grow in height more slowly than the related diploid variety, and frequently are somewhat shorter than diploids of the same age.

Recently Taylor (1941) became interested in the water relations of tetraploid and related diploid varieties of *Vinca,* and his comparative measurements of water absorption and transpiration indicate that the tetraploid strain developed by Schnell may prove to be generally desirable for cultivation in the southwestern part of the United States. The tetraploid strain and several interesting chimeras were given to the present writers for histogenetic studies, and grateful acknowledgment is made to Miss Schnell and Mr. Taylor.

The fundamental importance of apical meristem in problems dealing with growth of the shoot has been stressed recently by Jones (1937), Foster (1939), and Satina, Blakeslee, and Avery (1940). Except for an investigation of colchicine-induced periclinal chimeras of *Datura* (Satina, Blakeslee, and Avery 1940), apparently no comparative studies of the shoot apices of polyploids and related diploids have been made. The present investigation was undertaken in an effort to determine if the changed appearance of colchicine-induced tetraploid periwinkles could be correlated with visible changes in the structure and growth of the apical meristem.

METHODS

The shoot apices used for the present investigation were obtained from white-flowered plants grown from seed in the greenhouses at the University of Oklahoma. The tetraploid material was collected from the F_1 generation of the new strain induced by Schnell (1940). Schnell had treated the apices of two white-flowered plants with a colchicine-lanolin mixture (1:100). After this treatment the main axes died back and lateral, tetraploid branches were developed. Seeds collected from these tetraploid branches produced the F_1 plants here described. Because the flowers of *V. rosea* are normally self-pollinated, it was assumed that the new tetraploid variety would breed true. Such has proved to be the case, as is demonstrated by epidermal characteristics (figs. 2, 2A) and by chromosome counts made from pollen mother cells (figs. 3, 3A)[2] of the F_1.

Tischler (1931) has reported 8 chromosomes for the haploid phase of the normal diploid variety of *V. rosea,* and Simonet and Chopinet (1939) found 16 chromosomes in the corresponding phase of tetraploid varieties. Figures 3 and 3A in the present paper confirm the counts made by these earlier investigators.

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[2] Aceto-carmine preparations from which these photographs were made were prepared by Dr. O. J. Eigsti, University of Oklahoma, to whom the writers extend grateful thanks.

The materials were killed and fixed in formalin-acetic-alcohol (5 parts formalin, 7 parts glacial acetic acid, and 88 parts 60 per cent ethyl alcohol) and in Juel's solution (Korody 1937) under reduced pressure. Tertiary butyl alcohol was used for dehydrating and clearing (Cross 1937a), and the materials were embedded in "Tissue Mat." Serial sections were cut 8 μ in thickness; safranin and fast green (Cross 1937a) were used in staining. A Wratten A filter, no. 25, was used during photomicrography to emphasize the cell walls.

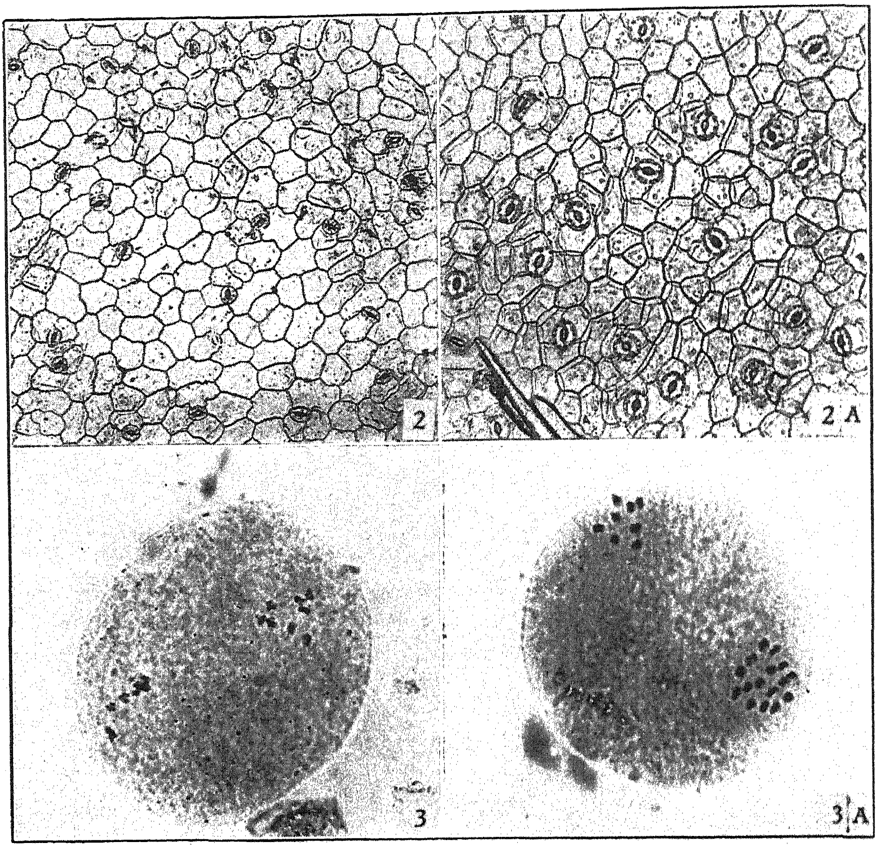

FIG. 2. Diploid epidermis. × 100. FIG. 2A. Tetraploid epidermis. Note that the tetraploid guard cells are considerably larger than the diploid but that the other epidermal cells are about the same size in each strain. × 100. FIG. 3. Diploid microspore mother cell immediately after reduction division, showing chromosomes in groups of 8. × 666. FIG. 3A. Tetraploid microspore mother cell immediately after reduction division, showing chromosomes in groups of 16. × 666.

GENERAL FEATURES OF THE DIPLOID SHOOT

Apparently the only published account of apical meristem in the genus *Vinca* is Schmidt's (1924) description of the shoot apex of *V. minor* L.

In this species there is a three-layered tunica and a central corpus with an irregular cellular pattern. The outer layer of the tunica divides only anticlinally and its derivatives develop into the epidermis of the shoot. The second and third layers of the tunica also divide only anticlinally at the summit of the meristem, but during leaf initiation periclinal divisions occur in the flanks, and the derivatives of these early periclinal divisions produce the internal portions of the leaf. Schmidt was able to demonstate that the derivatives of the second layer of the tunica produce the parenchymatous portions of the leaf, whereas the vascular tissue in this organ is formed from derivatives of the third or innermost layer of the tunica. In the shoot axis derivatives of the tunica produce the epidermal and cortical portions, but the stelar regions, except for the leaf traces, are derived from the corpus. Because the various layers of the tunica and the corpus of *V. minor* make such definite and precise contributions to the shoot axis, Schmidt regarded these growth zones as true histogens equivalent to those of Hanstein (1868) as follows: the first layer of tunica is the dermatogen, the second and third layers of tunica are the periblem, and the corpus is the plerome.

The shoot apex of *V. rosea* is elliptical in transection. The form and size vary during the course of a plastochron—the latter to a greater extent than the former. The "length," "width," and "height" of several apices, in various phases of development between periods of foliar initiation, were measured. As used in this paper the "length" and "width" refer respectively to the long and short axes of elliptical transections immediately above the axils of the youngest leaves. However, the measurements were made from median longitudinal sections. In each apex one dimension ("length" or "width," depending on the plane of the section) was obtained by direct measurement; the other necessarily was obtained by counting sections and multiplying by the thickness of the sections. The "height" was obtained by measuring the vertical distance from the summit to a straight line connecting the axils of the youngest leaves.

Immediately after the initiation of a pair of opposite foliar primordia, when the shoot apex is in a state of minimal surface area, the length of the apical meristem is usually about 70 μ, the width about 45 μ and height from 3 to 5 μ (figs. 4, 10, 15). During the ensuing plastochron the apex gradually increases in size, and attains its maximal surface area just prior to the initiation of the next pair of leaf primordia (figs. 4–10, 15–20). Measurements made at this stage indicate that immediately before leaf initiation the length of the apex is about 160 μ, the width 110 μ, and the height 45–50 μ. However these maximal dimensions are regarded as only approximately correct, because difficulty was experienced in deciding exactly when and between what points measurements should be made. The increased dimensions are attained in a uniform manner—that is, an increase in one dimension is correlated to a certain extent with increases in the others. At the end of each period of enlargement, when the meristem has reached its maximal surface area, a pair of opposite foliar primordia is differentiated in a plane parallel with the long axis of the transectional ellipse, and perpendicular to the plane of the next youngest pair of leaves (figs. 10, 13, 20). At this point it is interesting to note that the range of dimensions given for *V. rosea* is slightly greater than reported by Schmidt for *V. minor* (length 104 μ, width 36 μ, and height 10 μ during minimal surface area, and length 139 μ, width 97 μ, and height 42 μ during maximal surface area).

STRUCTURE OF THE DIPLOID SHOOT APEX DURING MINIMAL SURFACE AREA

Immediately after the initiation of a pair of foliar primordia, median longitudinal sections cut in any plane show that the apex consists of three rather distinct peripheral layers of cells which cap a central region characterized by a somewhat irregular cellular pattern (figs. 4, 15). The two outer layers constitute the tunica. The cells of the tunica divide only anticlinally at the summit of the meristem, but as is shown later, periclinal divisions occur in the flanking portions of the second layer of the tunica during foliar initiation. Frequently a centrally located large cell dominates each of these layers (fig. 18). The third layer at the apex (fig. 4) is the first layer of the corpus. It maintains its identity for a variable period of time after the initiation of foliar primordia, but sooner or later the constituent cells split periclinally (figs. 5, 16) throughout its extent, and often this phenomenon occurs in such a regular manner that four layers of cells may be distinguished at the apex (figs. 6, 17), i.e., two layers of tunica and two of corpus. The layering is remarkably evident immediately beneath the summit,

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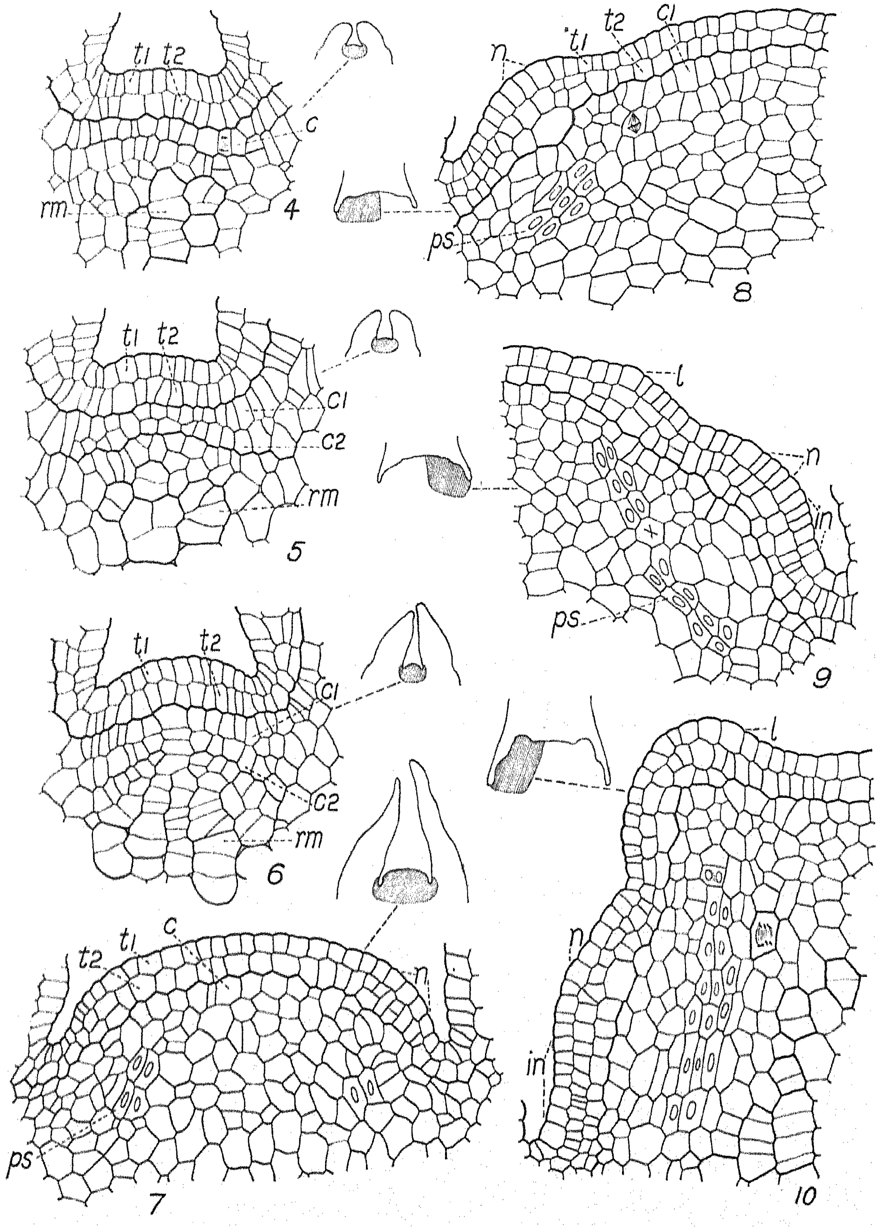
Explanation of figures 4–10

FIG. 4. Longisection of apical meristem of *V. rosea* in early stage of plastochron, cut parallel with plane of youngest pair of leaves; *t1*, first layer of tunica; *t2*, second layer of tunica; *c*, corpus; *rm*, rib meristem. FIG. 5. Longisection of apical meristem in later stage of plastochron cut in same plane as fig. 4, showing periclinal splitting of cells in first layer of corpus; *c1*, first layer of corpus; *c2*, second layer of corpus. FIG. 6. Longisection of apical meristem cut in same plane as figs. 4 and 5, showing still later stage in plastochron. Note intercellular spaces in rib meristem. FIG. 7. Longisection of apical meristem immediately after foliar initiation, cut perpendicular to plane of youngest pair of leaves; *n*, nodal region; *ps*, provascular tissue. FIG. 8. Longisection of apical meristem cut in same plane as fig. 7, showing later stage in development of nodal region and provascular tissue. Note that provascular tissue is separated from derivatives of the tunica by cells of the corpus. FIG. 9. Longisection of apical meristem showing periclinal divisions in T–2 associated with origin of foliar promordium; *l*, foliar primordium; *n*, nodal region; *in*, internodal region. Note vascular tissue in two youngest internodes separated by undivided cell marked X. FIG. 10. Longisection of apical meristem showing later stage of foliar primordium and further development of nodal and internodal regions. Note acropetal differentiation of provascular tissue. × 325.


t1
t2
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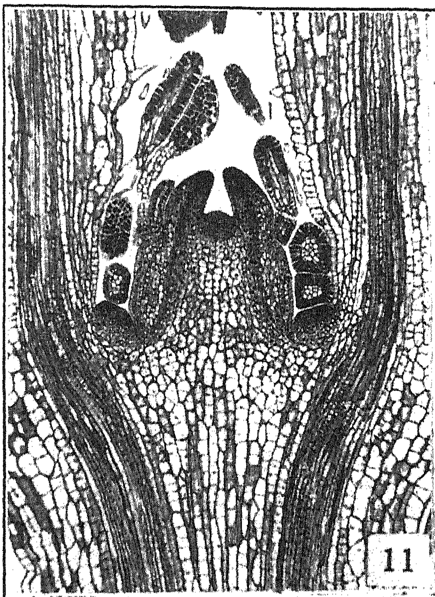
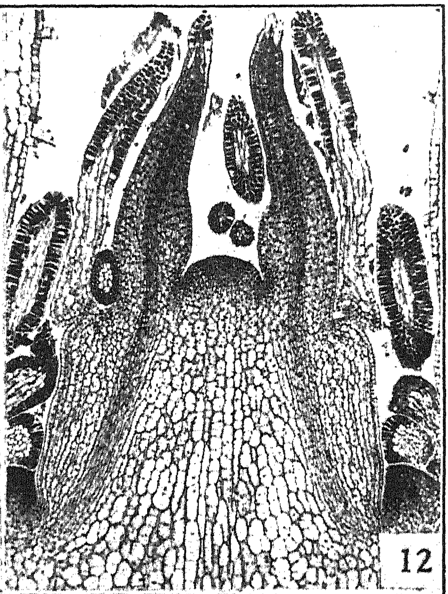
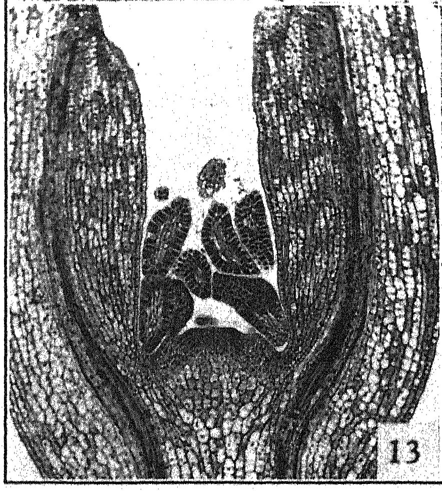
but frequently, because of the presence of oblique walls, it may not be seen in the flanking regions of the corpus. For convenience these four layers are hereafter designated as T–1 (first layer of tunica), T–2 (second layer of tunica), C–1 (first layer of corpus), and C–2 (second layer of corpus). A comparison of the description and figures given here for *V. rosea* with those by Schmidt (1924) for *V. minor* reveals the interesting fact that the tunica of *V. rosea* consists of one less layer of cells than is found in *V. minor.* A similar variation in the structure of the tunica amongst different species of the same genus has been reported for *Viburnum* (Cross 1937b, 1938) and *Veronica* (Schmidt 1924).

GROWTH OF THE DIPLOID SHOOT APEX

An idea of the changes that occur in the apical meristem during the course of a plastochron, including the initiation of foliage leaves, may be obtained by studying figures 4–10 and 15–20. In figure 4 the narrow, columnar appearance of the cells in T–1 and T–2 provides evidence of recent mitotic activity. Although only anticlinal divisions occur in the tunica, the summit of the meristem is gradually elevated (increased in height) during the plastochron. It is apparent in figure 5 that this increase in height is a result of cellular activity in the corpus. All the cells of the first layer of the corpus except one cell near the center have divided periclinally (thus forming C–1 and C–2), and a slight growth of the derivatives has thrust the apex of the shoot upward somewhat. Below C–2 the cellular pattern is irregular in all figures. In figure 5 several groups of genetically related cells, each clearly derived from a single mother cell, and oriented in a manner suggestive of a rib meristem, may be seen in the central portion of the corpus. The mother cells of the rib meristem are derivatives of C–2, although formed perhaps during the preceding plastochron. In figure 6 a highly organized rib meristem may be seen, consisting of chains of cells which diverge from a region immediately below the central portion of C–2. The derivatives of the rib meristem augment the pith. Thus during the early stages of growth following foliar initiation the apical meristem may be regarded as consisting of four layers which cap the mother cells of a rib meristem. The relatively "shallow" nature of the apical meristem is apparent in figure 11, where the abrupt transition from densely cytoplasmic layers to highly vacuolate rib-meristem is striking. Except for relatively infrequent periclinal divisions (fig. 7), C–1 divides anticlinally during the plastochron, and as a result it appears as a discrete layer after the primordia of the next pair of leaves are initiated. However, the cells of C–2 divide extensively in various planes, and the derivatives form a massive core of tissue as the apex increases in size. Continued division and growth of the derivatives of C–2 elevate the surface of the meristem and generally thicken the meristem in vertical as well as lateral directions (figs. 7, 19).







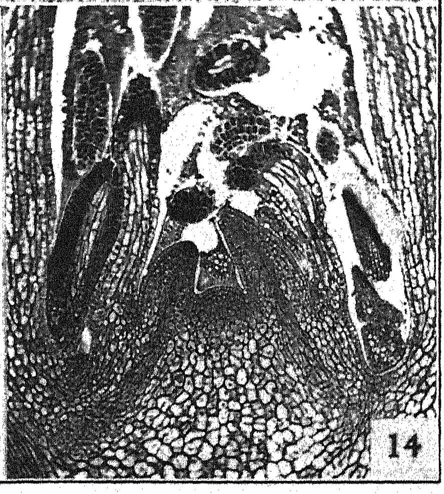
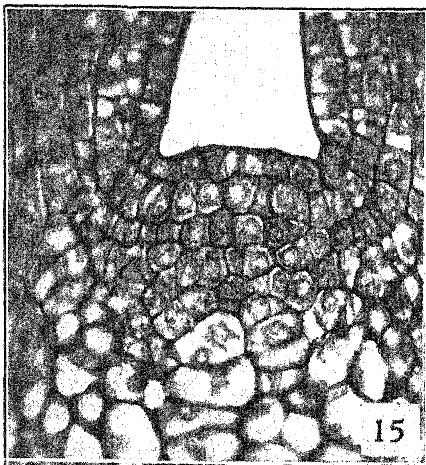


FIG. 11. Longisection of shoot apex showing apical meristem, young foliar primordia, young internode, axillary buds, glandular hairs. FIG. 12. Longisection of shoot apex cut perpendicular to plane of youngest foliar primordia. FIG. 13. Longisection of shoot apex in same stage of development as represented by fig. 12 but cut perpendicular to fig. 12. Note very young foliar primordia and lateral to them, young nodal and internodal regions. FIG. 14. Longisection of a colchicine-induced, tetraploid shoot apex of approximately the same stage of development as the one represented in fig. 11. × 70.

For a clearer understanding of the interrelated functions of the tunica and corpus in the growth of the shoot axis, it will be helpful to refer to figures 7 and 19, prepared from sections cut parallel with the longer transectional axis of the enlarging meristem shortly after leaf initiation (the youngest leaves are not in the plane of the paper). In these figures the layers of the tunica, except for the larger number of cells in each layer, are similar structurally to those seen in the previous figures, although the curvature of the apex is greater. Divisions in T–1 obviously had been entirely anticlinal up to the time that the material was fixed. Similarly in T–2 anticlinal divisions had prevailed at the summit, but in the margins or flanks of the meristem several cells in T–2 show evidence of having divided periclinally. Upon casual observation it might be supposed that such pericilinal divisions represent preliminary stages in the initiation of a new pair of foliar primordia. However, this is not the case; on the contrary, the periclinally divided cells of T–2 in figures 7 and 19 are related to the recently initiated, opposite foliar primordia, which are oriented in a plane perpendicular to that of the paper. In other words, these periclinal divisions are concerned with the development of the nodal and possibly the internodal portions of the shoot axis which are located immediately between and below the margins of the opposite leaf bases. From a study of many sections similar to those represented in figures 7 and 19 it appears that periclinally dividing cells in T–2 extend as a ring or ellipse throughout the entire circumference of the shoot apex during foliar initiation. In the plane of the long axis the derivatives contribute to the tissues of the young leaves; in the plane of the short axis they contribute to the cortex of the node and internode. This developmental feature was not described by Schmidt for *V. minor*. Figure 8 represents a later stage in the development of the nodal and internodal portions of the shoot axis which are associated with the youngest foliar primordia. The ridge-like appearance of such regions as seen in longitudinal sections is confusingly suggestive of foliar primordia, and only when a series of stages

Explanation of figures 15–20

FIG. 15. Longisection of shoot apex in early stage of plastochron cut parallel with plane of youngest leaves. Note three distinct layers at summit of meristem. FIG. 16. Longisection cut in same plane as fig. 15 but slightly later in plastochron, showing periclinal splitting of cells in first layer of corpus. FIG. 17. Longisection of apical meristem in still later stage of plastochron cut in same plane as figs. 15 and 16. Note transformation of derivatives of C–2 into rib meristem. FIG. 18. Similar to 16, showing large cells dominating first and second layers of tunica. FIG. 19. Longisection of apical meristem cut perpendicular to plane of youngest foliage leaves; periclinal splitting in flank of T–2 is associated with origin of node and associated internode of youngest leaves; *p*, provascular tissue. FIG. 20. Longisection apical meristem cut parallel with youngest foliar primordia, showing development of nodal and internodal region and vacuolation of cells in cortex; *p*, provascular tissue; *c*, cortex of young internode. Figs. 15–19, ×530; fig. 20, ×250.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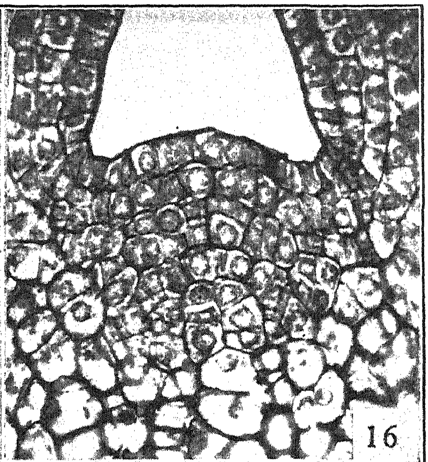
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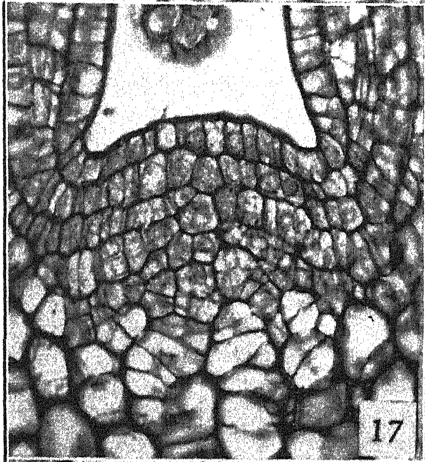
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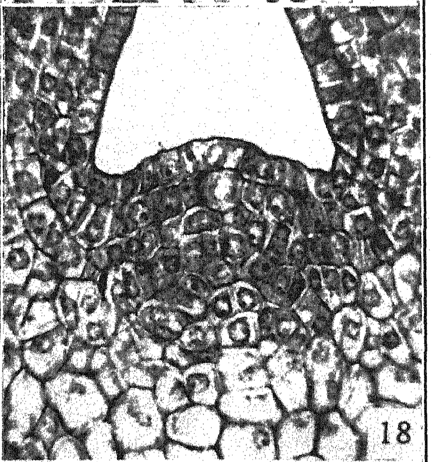
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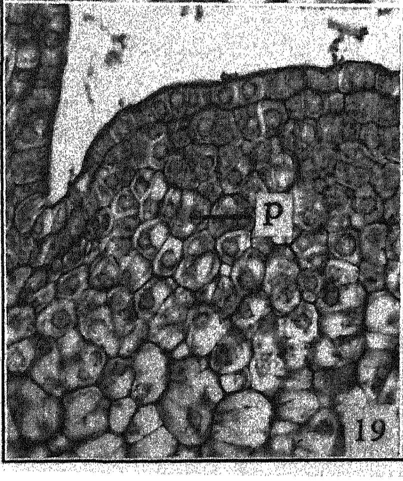

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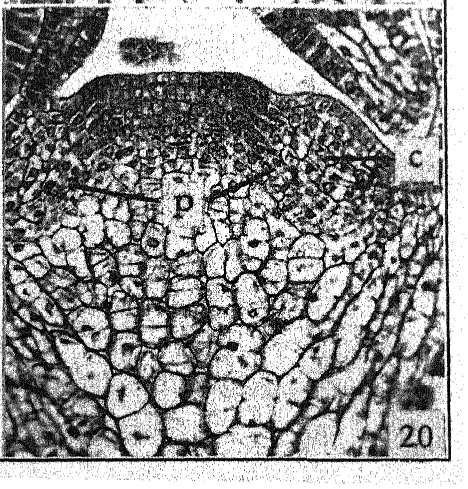

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such as those represented by figures 7–10 and 20 is studied, does the real significance of the region become apparent.

To the left, in the youngest internode represented in figures 7 and 19, elongated cells indicating the origin of provascular tissue may be seen. Figures 8, 9, and 10, prepared from apices more advanced in the plastochron, confirm this interpretation. It is obvious that the provascular tissue of the axis is initiated from lateral derivatives of the corpus, which is in agreement with Schmidt's account of *V. minor;* however, in contrast to *V. minor* the provascular tissue in *V. rosea* is not differentiated immediately adjacent to derivatives of the tunica, but is separated from these by other derivatives of the corpus. Therefore, the corpus contributes to the cortex as well as to the stele of *V. rosea*, and accordingly is not to be regarded as equivalent to Hanstein's plerome.

When the length (long dimension as seen in transection) of the shoot apex is approximately 160 μ, new foliar primordia are differentiated in a plane perpendicular to the last pair, and they appear as small crescent-shaped protuberances located immediately centrad to the bulging nodal and internodal areas previously described. In figure 9, it may be seen that the earliest stages in foliar initiation are correlated with periclinal divisions in T–2. In later stages (fig. 10) the corpus extends as a core into the base of the primordium. The extent to which the corpus contributes to the tissues of the leaf was not determined precisely, but the results of studies by Johnson (1941) indicate that much of the foliar vascular tissue, at least that in the proximal regions, is derived from this growth zone. In *V. minor* derivatives of the corpus are not involved in foliar initiation, for in this species the foliar primordium is a product entirely of the tunica. The function of the third layer of the tunica of *V. minor*, i.e., the production of the vascular tissue of the leaf, is performed by the first layer of the corpus (however, the third layer of meristem) of *V. rosea*. The primordia grow vertically, perpendicular to the summit of the apical meristem. The elongated cells in the corpus (and youngest internode) near the base of the young foliar primordium in figure 9 represent the initiation of a provascular strand with which the leaf trace will be continuous. Similar provascular tissue may be seen in the second internode below, separated from that above by a single nodal cell marked X. As shown in figure 10 these two provascular strands become continuous; and at the upper limit of the strand a periclinally dividing cell, associated with the vertical differentiation of the provascular tissue into the leaf base, is evident. Thus the leaf trace of *V. rosea* apparently differentiates only in an acropetal direction, rather than both acropetally and basipetally, as described commonly for angiospermous genera.

THE SHOOT APEX OF TETRAPLOID PLANTS

In all basic structural features the apices of the tetraploid shoots are practically identical with those of the related diploid strain. A two-layered tunica capping a central corpus is easily demonstrated (figs. 22, 24). The behavior of the tunica and corpus during the course of a plastochron, and the cellular contributions of these growth zones during the initiation of leaves, nodal and internodal portions, provascular tissue, pith, cortex, and epidermis are the same as described for the diploid variety; therefore, a second description will not be necessary.

However, it is apparent from a comparison of figures 11 and 14 that the tetraploid apices are considerably more massive than those of diploid shoots. Figures 21 and 22, prepared from diploid and tetraploid apices respectively, show that this is true not only of the apical meristem, but of the foliar primordia as well. The young tetraploid leaf in figure 22 is considerably thicker than the corresponding diploid leaf in figure 21, although both leaves are of approximately the same height, and both figures have the same magnification.

Havas (1937), Eigsti (1938), Levan (1938), and others have reported that the increased size of a plant organ after treatment with colchicine is a result of increased cellular size rather than an increase in number of cells. It is apparent from only a casual comparison of tetraploid and diploid shoot apices (figs. 21–22, 23–24) that the increased size of the tetraploid meristem and foliar primordia is a result of increased cellular size rather than increased cellular number. It is further apparent that the *lateral* dimensions of the tetraploid cells have been increased more noticeably than the *vertical* dimensions. This is shown strikingly by figures 23 and 24, representing diploid and tetraploid meristem respectively, photographed with identical magnifications. In an effort to determine precisely what effect colchicine has upon the form and structure of the cells in the apical meristem of *Vinca*, a number of careful measurements were made of anticlinal walls, periclinal walls, and nuclei in the growth zones of both the diploid and tetraploid varieties. Shoot apices in various stages of growth following foliar initiation were selected for measuring. The measurements were taken only from T–1, T–2, and C–1 of each apex, because these regions are the primary centers of growth in the apical meristem. The average lengths of the periclinal and anticlinal walls in each layer were determined and the results for several apices are recorded in table 1.

It was found from measurements made of a series of diploid apices that the average dimensions of the cells in T–1, T–2, and C–1 do not vary greatly during the course of a plastochron (table 1). The greatest variation occurs in the anticlinal walls of C–1, as is shown by a comparison of apices 1, 2, and 3 in table 1. However, this is easily understood because the first layer of the corpus divides periclinally throughout its extent early in the course of a plastochron, and immediately after this division, before the derivatives have enlarged, the vertical dimensions of the cells in the new C–1 (upper layer of derivatives) are considerably smaller than at other stages during the plastochron.

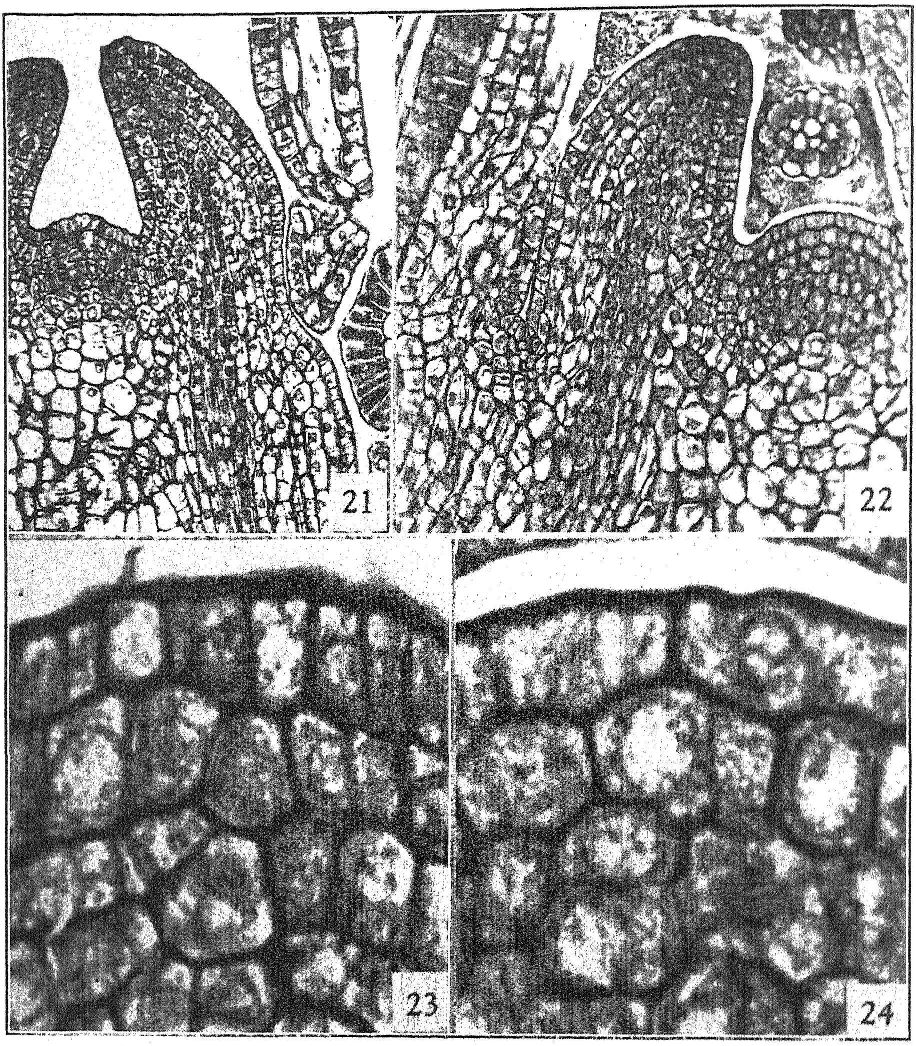

FIG. 21. Shoot apex and foliar primordium of diploid plant. FIG. 22. Shoot apex and foliar primordium of tetraploid plant. Note that the apical meristem is wider and not appreciably deeper than in the diploid. × 221. FIG. 23. Summit of apical meristem of diploid plant. FIG. 24. Summit of apical meristem of tetraploid plant. Note that the cells of the tetraploid have greatly increased lateral dimensions but that the vertical dimensions are approximately the same as those of the diploid. × 1105.

Measurements of the corresponding layers in tetraploid apices reveal the interesting fact that the anticlinal walls in T–1 and T–2 are certainly no greater in *vertical* dimensions than are those of the diploid meristem. As a matter of fact, the average dimensions given in table 1 are somewhat less than those of the diploid. However, in C–1 the cells have slightly but definitely greater vertical dimensions in the tetraploid apices, as shown by measurements of the anticlinal walls. The *lateral* dimensions of the cells in all three layers are considerably greater in the tetraploid apices, as is shown by the average dimensions of the periclinal walls given in the table. From the figures here given it would appear that treatment with colchicine has increased the lateral dimensions of the cells in T–1 68.1 per cent, those in T–2 43.6 per cent, and those in C–1 58.9 per cent. This has resulted in considerably widened apices, but not noticeably deeper ones—because the vertical dimensions of the constituent cells have not been greatly altered.

The nuclei in the cells of both diploid and tetraploid apices occupy nearly all of the internal portions of the cells. Twenty-four nuclei from each strain were measured at random from T–1, T–2, and C–1. The diploid nuclei had an average size of 6.7 μ as compared with 8.9 μ for the tetraploid—representing a size increase of nearly 33.3 per cent following treatment with colchicine.

The tetraploid plants used in the present investigation have shorter and more massive stems, thicker and greener leaves, and somewhat larger flowers than their diploid ancestors. In the following paragraphs it is shown how all of these structural features seen in the mature plants, except those pertaining to the flower, are correlated directly with visible differences observed in the tunica and corpus.

The effect of colchicine upon the apical meristem of *V. rosea* is to increase the lateral dimensions of the cells to an extent varying roughly from one-half to two-thirds. This means that the entire apex is broadened in an amount equivalent to the sum of the increased dimensions of the constituent cells. A thicker pith and a generally more massive stem is the result. The vertical dimensions of the cells in the apical meristem are not increased however, and the mitotic rate of the tetraploid cells is apparently somewhat less than that of the diploid tissue. Both of these latter features are correlated with the fact that the tetraploid stems are thicker but not longer, and often are shorter, than the diploid.

The thicker, greener leaves of the tetraploid plants may be correlated similarly with the increased lateral dimensions of the apical meristem, when the method of their initiation is considered. The initial elevation of the foliar primordium occurs as a result of periclinal division in the cells of T–2, and therefore the elevation is in a direction perpendicular to the surface of the apical meristem. In the tetraploid apices the lateral dimensions of the cells of T–2 (T–1 and C–1 as well) have been increased markedly, and the derivatives of T–2 which constitute the internal portions of very young foliar

TABLE 1

Dimensions of cells in diploid and tetraploid meristems

Shoot apex number	Average dimensions of anticlinal and periclinal walls in T–1, T–2, and C–1								
	T–1			T–2			C–1		
	No. cells	Ant. walls	Per. walls	No. cells	Ant. walls	Per. walls	No. cells	Ant. walls	Per. walls
Diploid 1	12	9.1	4.5	11	9.5	5.5	11	8.3	5.5
Diploid 2	12	8.0	4.4	12	9.2	4.5	12	6.3	5.0
Diploid 3	14	8.3	5.0	15	8.9	5.1	13	8.0	5.5
Diploid 4	20	8.6	4.9	19	8.7	6.9	18	6.5	6.3
Diploid Average	14.5	8.5	4.7	14.3	9.0	5.5	13.5	7.3	5.6
Tetraploid 1	18	8.2	7.4	16	8.1	8.3	13	8.8	9.6
Tetraploid 2	12	7.9	7.1	11	9.0	7.5	12	7.4	7.3
Tetraploid 3	13	8.5	9.3	11	9.5	8.1	13	7.8	9.7
Tetraploid Average	14.3	8.2	7.9	12.7	8.9	7.9	12.7	8.0	8.9
Average percentage increase following treatment with colchicine		–3.5%	68.1%		–1.1%	43.6%		9.6%	58.9%

primordia accordingly have greater lateral dimensions than the corresponding cells in diploid foliar primordia of a comparable height. This results in tetraploid foliar primordia with considerably greater radial thickness, a feature which perhaps is correlated with the thicker and greener mature leaves. The possibility of a similar correlation of meristem characters with the somewhat larger tetraploid flowers will be investigated later.

DISCUSSION

The need for comprehensive information concerning the apical meristem in species of angiosperms is borne out by the fact that three (*Veronica*, *Viburnum*, and *Vinca*) of the relatively small number of investigated genera have species in which the structure of the shoot apex is not uniform with respect to the quantitative relationships of the tunica and corpus.

In *V. minor* three layers constitute the tunica—in *V. rosea* there are only two; however, as far as the fundamental features of growth in the two species are concerned, there are no great differences, for in each species derivatives of the outer three layers at the shoot apex form the foliar primordia and cortical tissues while the stele is a product of the more internally placed meristem. Thus the outer layer of the corpus makes essentially the same cellular contributions in the shoot of *V. rosea* as are made by the third layer of the tunica in *V. minor*.

Schmidt (1924) has emphasized that the relative contributions of the tunica and corpus to leaf or bud initiation are dependent upon the quantitative relationships of these growth zones at the shoot apex. Schmidt's conclusion is supported by the results of the present investigation, for clearly the extent to which each of the growth zones contributes to the leaf and shoot axis in the genus *Vinca* is dependent upon their quantitative relationships in the apical meristem of each species, i.e., upon the number of layers in the tunica of each species. It would seem that the variations in quantitative relationships of the tunica and corpus that occur so commonly in the shoot apices of angiosperms may be of phylogenetic significance mainly with respect to problems of speciation. From a practical point of view they may prove to be of considerable significance in understanding problems associated with the origin of new varieties of plants, particularly the induction of new varieties by treatment with colchicine and other drugs.

In contrast to the procedure commonly described for seed plants, the leaf traces of *V. rosea* are differentiated acropetally into the foliar primordia and from the beginning are in continuity with provascular tissue previously formed in the two internodes and intervening internode immediately below. A similar acropetal differentiation has been described for the phyllode traces of *Acacia* (Boke 1940) and for the leaf traces of *Sequoia* (Crafts 1940). From an examination of a large number of genera of vascular plants, Wetmore[3] has concluded that strictly acropetal differentiation of leaf traces may be much more prevalent than has been suspected heretofore, and doubtless the subject should receive additional investigation. In this connection it is interesting to recall that Grégoire (1938) stressed the acropetal differentiation of provascular traces into floral parts, and used this feature in support of his idea that floral parts and foliage leaves are not homologous structures.

It is generally known that chromosomal number and cellular size may be increased by treatment with colchicine. The shoot apices of the induced tetraploid strain of *V. rosea* provide evidence that colchicine may also influence the *shape* or *form* of the cells in treated meristem and thereby affect the form of the adult plant. Similar formative effects were not reported for the apical meristem in tetraploid plants of *Datura* (Satina, Blakeslee, and Avery 1940), and it is clear that additional investigations are necessary before we can hope to understand the action and appreciate the possibilities of the drug in plant breeding.

SUMMARY

The shoot apex of *V. rosea* is described and compared with that of *V. minor* (Schmidt 1924).

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[3] Private communication with Ralph H. Wetmore, Harvard University.

The shoot apex of *V. rosea* consists of a two-layered tunica and a central corpus, in contrast with that of *V. minor* for which a three-layered tunica has been described. With the exception of the outer layer of the tunica which produces the epidermis, the growth zones do not make precise contributions to the shoot axis, and therefore Hanstein's histogen-theory is not applicable to *V. rosea*.

Although the quantitative relationships of the tunica and corpus differ in the two species, the general features of growth at the shoot apices are similar, for in each species the outer three layers of the apical meristem make essentially the same contributions to the foliar primordia and shoot axis. Thus the functions of the tunica and corpus are correlated with their quantitative relationships.

The leaf traces differentiate acropetally into the bases of foliar primordia, rather than both acropetally and basipetally as is commonly reported for angiosperms.

The shoot apices of a colchicine-induced tetraploid strain of *V. rosea* are similar to those of the diploid parent in the quantitative relationships of the tunica and corpus. The apical meristem of the tetraploid plants is considerably wider than that of the related diploids, but the vertical dimensions are approximately the same. The increased width of the tetraploid apices is a result of increased lateral dimensions of the cells in the apical meristem. Cellular measurements indicate that treatment with colchicine as an average increases the lateral dimensions of the cells in T–1 about 68 per cent, those in T–2 43 per cent, and those in the first layer of the corpus 59 per cent. Significant differences in the vertical dimensions of cells of diploid and tetraploid meristems were not noted. The nuclei in tetraploid meristem are, as an average, approximately one-third larger than those of the diploid.

It is emphasized that colchicine affects the *shape*, as well as the size and chromosomal number, of the cells in the apical meristem of *V. rosea*. Visible changes in the meristem following treatment with colchicine are correlated with changes in the form of the adult plant.

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STUDIES ON AMERICAN HEPATICAE—III. VEGETATIVE REPRODUCTION IN BRYOPTERIS FRUTICULOSA

MARGARET FULFORD

(WITH THIRTEEN FIGURES)

Plants of *Bryopteris fruticulosa* Taylor collected at Punta Gorda, British Honduras, in November, 1932, exhibit an interesting example of vegetative reproduction by means of miniature shoots. These young shoots may be considered of two sorts depending on their place of origin on the plant, although they do not differ in their structure. The one sort originates from individual cells of the leaf and will be designated as leaf-cladia.[1] These are identical with the "Brutsprösschen" of Degenkolbe (2) and other authors. The other sort, the stem-cladia, originates on the stem and occupies the same position on the stem as the sexual branches. These belong to the category "Brutäste."

The leaf-cladia usually arise on the dorsal side of the ordinary, persistent leaves, especially after they are badly weathered or "eroded." They occur on any portion of the surface of the leaf and show no periodicity in their development, one leaf often bearing shoots of different sizes (see figure 1). They also occur on the male bracts.

This type of vegetative reproductive body on persistent leaves has been described in *Plagiochila* (1) and *Bazzania* (10). It is also frequent in many species with caducous leaves, associated with the caducous leaves. Evans (6) has described them in several tropical American genera, and more recently Degenkolbe (2) has given a comprehensive summary of "Brutsprösschen" in Hepaticae.

An ordinary leaf cell becomes more chlorophyllose than those adjacent and divides by means of a wall at right angles to the surface of the leaf (fig. 2), and one or both of the newly formed cells bulge on the dorsal surface (fig. 3). Then from one of these new cells one or two cells are cut off by transverse walls parallel to the leaf surface, so that a very short filament is formed. An apical cell with three cutting faces develops from the end cell after a few cells are cut off through anticlinal divisions. The new shoot is formed by the activities of this cell. The first cells cut off have bulging sides and can easily be distinguished even after the shoot has attained considerable length (figs. 4, 5). The first two leaves are very rudimentary, consisting of only three cells each. Each succeeding leaf becomes larger, and on the fifth or sixth leaf rudimentary lobules become evident. These, too, become larger on succeeding leaves and are well developed on the ninth or tenth leaves. The typical (mature) leaves of these shootlets have more or less the same outline as the leaves of the parent plant, but they are, of course, very small, show no evidence of teeth on the margins, and have proportionately larger lobules. The first underleaf usually arises after the formation of the fifth leaf and is very rudimentary (see figure 5), triangular, and consists of three cells. Each successive one is larger and more completely developed. The mature underleaf is oblong and emarginate.

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[1] Cladium (κλαδίον, diminutive of κλάδος, a branch or slip) is here proposed as a name for the small detachable branches which are effective in vegetative reproduction. The word was suggested by Dr. H. W. Rickett.

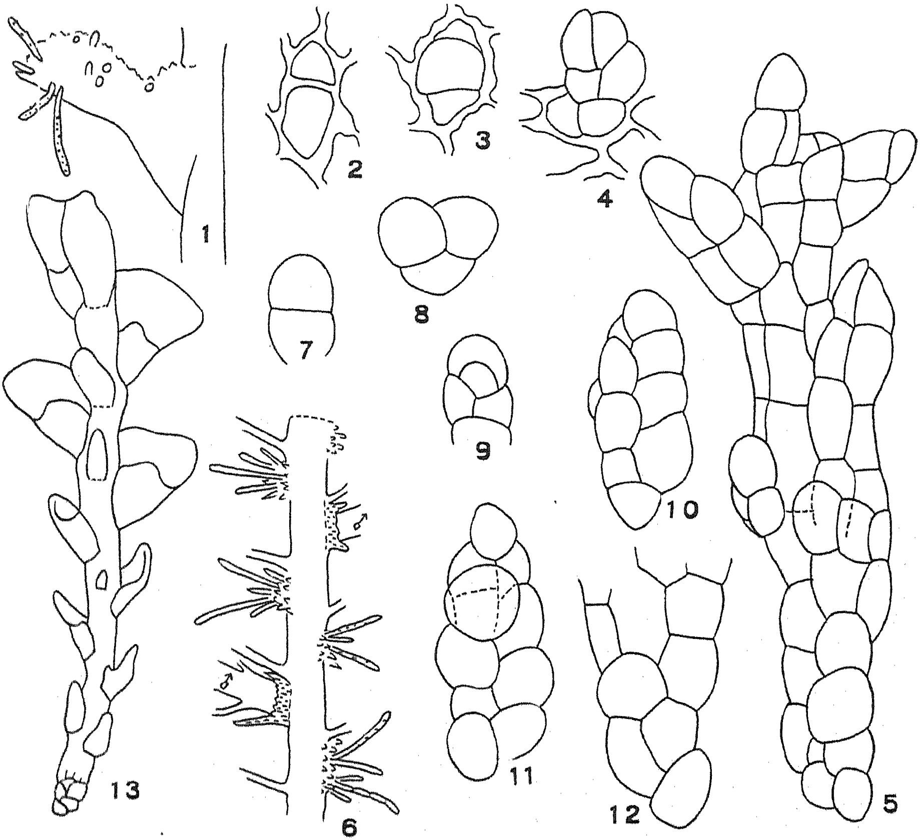

FIG. 1. Sketch of an "eroded" leaf showing brood shootlets on the dorsal surface. FIG. 2. A cell which has undergone the initial division in the formation of the propagule, ×375. FIGS. 3–4. Early stages in its development, ×375. FIG. 5. An older brood shoot showing the earliest leaves, ×375. FIG. 6. Diagram of a branch showing the position of the male branches and the tufts of brood branches just below the leaves. FIGS. 7–11. Stages in the development of the brood branch, ×375. FIG. 12. Basal portion of an older brood branch showing the rounded cells and the attachment cell, ×375. FIG. 13. A brood branch with well developed leaves and underleaves, ×90.

The stem-cladia are much more abundantly produced, often hundreds of them occurring on a single stem. They are characteristically on the branches but are not uncommon on the main axis. They are produced in tufts of from ten to thirty or more just below a leaf, in the position of the sexual branches, often on the same axis with them (see figure 6).

The sexual branches are of the *Radula* type, that is, they "arise in a cortical cell adjacent to the base of a leaf on the basiscopic side and in the ventral portion of the segment" (8) and each has a well-developed sheath at its base. The tufts of stem-cladia arise in a similar position but do not develop such sheaths.

The individual branchlets of the tuft originate in disc-like areas of cortical cells just below the leaves. A transverse section of the stem shows a medulla fifteen or more cells in diameter, surrounded by a cortex of one layer of cells more or less rectangular in outline, not unlike the structure of the stem of *B. filicina* described by Evans (9). The inner cells of the medulla have relatively thin walls and are little pigmented, but the cells of the outer two or three rows, those nearest the cortex, have very thick walls and are deeply pigmented an orange-brown color. The cortical cells are larger, with thinner walls, and are a little less pigmented than the adjacent medullary cells. The cortical cells which give rise to the propagula are somewhat larger than those adjacent to them and do not have the typical deep, orange-brown color. In addition, the adjacent rows of cells of the medulla have thin walls and lack the usual pigmentation.

In the formation of the stem-cladia a cortical cell of the sort just described becomes packed with material and divides by means of a wall at right angles to the surface. The new cells bulge out and each one through a wall parallel to the periphery of the stem becomes two cells. The outer cell, by a series of divisions at right angles to the stem axis forms a mass of cells. Each one of the cells thus formed is capable of producing a new shootlet, through the formation of a few-celled filament, which in turn produces the apical cell of the new shoot, after the manner described for the development of the leaf-cladia from cells of the leaves (see figures 7–10). As in the latter, the early cells cut off are rounded in outline and irregularly arranged; the early leaves are rudimentary, consisting, for the most part, of only three or five cells; the well developed lobules appear on the ninth or tenth leaves; and the underleaves are at first very rudimentary, but successive ones become narrowly ovate, and finally oblong and emarginate (fig. 13). The branchlets often become more than 1.5 cm. in length while yet attached to the stem. The point of attachment is a single cell (see figures 5, 10–12) and the branchlets are easily separated by a slight movement. The break is schizolytic. Although there was no evidence in the material examined that these branchlets grow into normal plants, without doubt propagation by this method frequently occurs.

These stem-cladia are much less highly specialized than those described by Evans (3, 4, 5) for *Leptolejeunea, Drepanolejeunea* and *Odontolejeunea*, since they do not arise singly, possess sheaths, or develop the radicelliferous discs found in those genera. Degenkolbe (2) has discussed the development of "Brutäste" in his summary of the brood organs in hepatics. Similar slender filiform branches have also been noted in *B. tenuicaulis* Tayl. (7).

In addition to the above mentioned material from British Honduras in the Missouri Botanical Garden, plants with similar stem-cladia have been collected at Mirador, Mexico, by F. Müller; the east Coast of Guatemala, by Sereno Watson no. 58c; and in Bolivia by White (Mulford Exp. Amazon Basin no. 2133a) and are in the collections of the New York Botanical Garden.

The writer wishes to express her appreciation to Dr. A. W. Evans for his helpful criticism.

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NORTH AMERICAN RANUNCULI—III[1]

LYMAN BENSON

The first article in this series of five (Bull. Torrey Club **68**: 157–172. March, 1941) includes a key to the species of the section *Chrysanthe* of the subgenus *Euranunculus* and discussion of the first seven species. The other eleven species of the section are discussed in the second article (Bull. Torrey Club **68**: 477–490. October, 1941). This article deals with the sections *Echinella* and *Epirotes*. The delimitation of subgenera and sections was published in a paper entitled "The North American Subdivisions of *Ranunculus*" (Am. Jour. Bot. **27**: 799–807. 1940).

SECT. 2. ECHINELLA DC.

KEY TO THE SPECIES

Achenes with spines on the faces or margins.
- Mature achenes 5–7 mm. long, the spines straight; petals at least 4 mm. long.
  - Achenes with the margins produced into long spines; nectary scale not forming a pocket, broader than the adjacent part of the petal .... 20. *R. arvensis.*
  - Achenes without spines on the margins, the faces spiny; nectary scale forming a pocket, much narrower than the adjacent part of the petal .... 21. *R. muricatus.*
- Mature achenes 1–2 mm. long, the papillae on the faces produced into hooked spines; petals 1–2 mm. long .... 22. *R. parviflorus.*

Achenes with no spines but the faces papillate, 1–2 mm. long.
- Petals 1–2 mm. long; papillae of the achenes produced into hooked hairs; sepals not reflexed .... 23. *R. hebecarpus.*
- Petals 8–9 mm. long; papillae of the achenes not produced into hairs; sepals reflexed .... 24. *R. sardous.*

20. RANUNCULUS ARVENSIS L. Sp. Pl. 555. 1753.

Waste ground and ballast; European weed; naturalized in North America; Yamhill and Marion Counties, Oregon; "Southern" Oregon; Potter Valley, Mendocino County and Mt. Bullion, Mariposa County, California; Grangeville, Idaho; Smithfield and Newton, Utah; metropolitan New York and New Jersey; Washington, D. C. Summer.

Type collection: "Habitat in Europae *australioris agris."*

21. RANUNCULUS MURICATUS L. S. Pl. 555. 1753. *R. echinatus* Vent. Jard. Cels. 73. 1800 (An. VIII of the French Revolution). *R. muricatus* var. *carolinianus* DC. Prodr. **1**: 42. 1824.

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[1] References in the first article of this series to Abrams' Illustrated Fora of the Pacific States **2**: 1940 are erroneous, since that work did not appear at the time scheduled late in 1940. The two new combinations, *Ranunculus canus* Benth. var. *laetus* (Greene) L. Benson and *R. canus* var. *ludovicianus* (Greene) L. Benson, should be considered as published in the Bulletin of the Torrey Botanical Club **68**: 170 and 171. 1941, instead of in Abrams' Flora.

Meadows, stream and lake borders, and vernal rivulets at low elevations; Europe; naturalized in North America; Seattle, Washington; Newport, Port Orford and Myrtle Creek, Oregon; Del Norte, Lake, and Butte Counties to San Mateo, Contra Costa, and Stanislaus Counties, California; Arkansas; Coastal Plain from Texas to South Carolina. April and May.

Type collections: (1) *R. muricatus*, "*Habitat in* Europae *australis fossis & humentibus.*" (2) *R. echinatus*, "Environs de Charles-town." Charleston, South Carolina. (3) Var. *carolianus*, "Carolina and Virginia."

22. Ranunculus parviflorus L. Sp. Pl. ed. 2. **1**: 780. 1762. *R. trachyspermus* Ell. Sketch. **2**: 65. 1816. *R. parviflorus* var. *dimidiatus* Krause, Beih. Bot. Cent. **32** (2): 330. 1914.

Waste ground; Europe; naturalized in North America; Humboldt County, California; Eastern Arkansas and Houston, Texas, to Lexington, Kentucky, Virginia, northern Georgia and extreme northwestern Florida; Peekskill, New York; Bermuda and St. David Islands, Bermuda; at 1,100 meters elevation in Jamaica. Summer.

Type collections: (1) *R. parviflorus.* "*Habitat in* Europae *australis.*" (2) *R. trachyspermus*, "Collected in St. John's Berkley, by Dr. Macbride." Near Savannah, Georgia. (3) Var. *dimidiatus, Krause* "No. 5567. Bei Virginia Beach am 13 Mai." Virginia, 1890.

23. Ranunculus hebecarpus Hook. & Arn. *R. parviflorus* L. var. Torr. & Gray, Fl. N. Am. **1**: 25. 1838. *R. hebecarpus* Hook & Arn. Bot. Beech. Voy 316. 1840. *R. hebecarpus* var. *pusillus* Brew. & Wats. Bot. Calif. **1**: 9. 1876.

Shade of trees at 100–1,000 or 1,300 meters elevation; Latah County, Idaho; Wawawai, Washington; Columbia River Gorge; occasional in southwestern Oregon; Siskiyou and Modoc Counties and the whole foothill region of cismontane California, except the seaward North Coast Ranges; Santa Catalina Island; northern Baja California and Guadaloupe Island. Primarily oak woodland. March to May.

Type collections: (1) Unnamed variety, Torr. & Gray, "California, Douglas!" (2) *R. hebecarpus*, "California—Supplement. Where not otherwise mentioned, it is to be understood that the following species are from the collection of Mr. Douglas. They were presented by the Horticultural Society of London, in whose service Mr. Douglas was at the time he gathered them." (3) Var. *pusillus.* No type given. It and the typical species were reported from the "coast-ranges and foot-hills of the Sierra Nevada." No plants of *Ranunculus hebecarpus* warrant segregation as a variety.

24. Ranunculus sardous Crantz, Stirp. Austr. Ed. 1. fasc. 2. 84. 1763. *R. parvulus* L. Mant. Pl. 79. 1767.

Waste places; Europe; naturalized mostly about seaports in North America; Columbia River at Portland, Oregon; Fortuna, Humboldt County, California; St. Louis; New York; Philadelphia; Norfolk and Meherrin River, Virginia; "Eastern" North Carolina; Savannah and Tybee Island, Georgia. May to July.

SECT. 3. EPIROTES (PRANTL) L. BENSON

KEY TO THE SPECIES

Roots not distinctly tuberous, if slightly fusiform-tuberous, the thickened portion not truncate, 0.5–2 or rarely 2.5 mm. in diameter; petals usually obovate or cuneate, rarely 2–3 times as long as broad.

Horizontal rootstocks not present.

Fruiting receptacle and head of achenes cylindrical or ovoid; achenes not stipitate or winged at the bases.

Stems 5 or more cm. long at fruiting time (measurement to the base of the highest pedicel).

Sepals not densely covered dorsally with reddish-brown hair.

Nectary scale ciliate (except rarely in *R. arizonicus*), the adjacent petal surface sometimes hairy also; achenes pubescent.

Stems scapose, rarely branching near the bases; nectary scale rectangular or nearly so; achene beak straight.

Each scape 4- or usually 8–12-flowered; dead leaf bases represented by numerous brown fibers; margin of the nectary scale free along the distal third; petals 2–3 times as long as broad, not emarginate; fruiting receptacle cylindrical, slender .... 29. *R. arizonicus.*

Each scape 1–3- or 4-flowered; dead leaf bases not markedly fibrous; margins of the nectary scale adnate to the petal for almost their entire length; petals nearly as broad as long, sometimes emarginate; fruiting receptacle ovoid or ovoid-cylindrical, stout ... 30a. *R. cardiophyllus var.*

Stems not scapose, branching near the bases; nectary scale obdeltoid; achene beak recurved .... 30. *R. cardiophyllus.*

Nectary scale and petal glabrous.

Margins of the nectary scale prolonged into 2 flaps attached most of their length to the blade of the petal, each flap 4–5 mm. long by 0.6 mm. broad; leaves dissected; plant practically glabrous. 31. *R. Eastwoodianus.*

Margins of the nectary scale not prolonged for more than 1 mm.

Fruiting receptacle 2–4 mm. long, 1–3 mm. in diameter; stems usually profusely branched and 8–25- or 60-flowered; achenes glabrous. (*R. arizonicus* is allied to this group of species as well as to *R. cardiophyllus.*)

Petals shorter than the sepals.

Achene beaks 0.1–0.3 or rarely 0.4 mm. long; petals two-thirds to five-sixths the length of the sepals; nectary scale laterally attached for its full length.

Herbage glabrous or nearly so; receptacle villous or rarely glabrous; leaves reniform, usually distinctly cordate; nectary scale notched (or truncate?) at the apex; head of achenes ovoid; achene beak 0.1–0.2 mm. long; bracts of 3 or 5 narrow divisions, these broadest at the middles; roots filiform, rarely thickened .... 25. *R. abortivus.*

Herbage villous; receptacle glabrous (rarely villous); leaves proximally truncate or almost attenuate; nectary scale truncate at the apex; head of achenes cylindrical or ovoid-cylindrical; achene beak 0.2–0.3 mm. long; bracts of 3–5 linear-oblanceolate divisions; some of the roots somewhat fusiform-thickened and some filiform on each plant. 26. *R. micranthus.*

Achene beaks 0.6–1 mm. long, curved or recurved; petals 1–1.5 mm. long, one-third to one-half the length of the sepals, broadly elliptic; nectary scale free laterally for half its length; bracts with 5 nearly linear lobes; roots all filiform; leaves reniform ...... 27. *R. alleghenienisis.*

Petals longer than the sepals; achene beaks 0.4–0.6 mm. long, straight; petals 6–8 mm. long, twice the length of the sepals; nectary scale attached laterally through its whole length, truncate; bracts with 3 oblanceolate divisions; some of the roots fusiform and 1.5–2.5 mm. in diameter; leaves reniform, the lobes relatively few. 28. *R. Harveyi.*

Fruiting receptacle 4–16 (or rarely only 3) mm. long, usually 3–9 mm. in diameter; stems sparingly branched, each bearing 1–3 or sometimes 7–9 or rarely 11 flowers.

Sepals and usually the pedicels densely tomentose.

Petals twice as long as the sepals .... 32. *R. pedatifidus.*

Petals scarcely longer than the sepals .... 33. *R. Sabinii.*

Sepals and pedicels glabrous or thinly pilose.

Achenes obovate.

Radical leaf blades ovate to orbicular, not broader than long; achene beak 0.8–0.9 mm. long; stems 3–7- or rarely 11-flowered; achenes 50–100 in a head 7–17 mm. long. .... 34. *R. inamoenus.*

Radical leaf blades reniform or semicircular, broader than long; achene beak about 0.3 mm. long; stems 1–3-flowered; achenes 20–45 in a head 4–6.5 mm. long .... 35. *R. Allenii.*

Achenes almost oblong.

Petals, when fully expanded, 3–5 mm. long, the sepals the same length; achene beaks recurved, 0.5 mm. long; basal leaves proximally cordate .... 36. *R. verecundus.*

Petals, when fully expanded, at least 60 per cent longer than the sepals, 8–18 (rarely 5) mm. long; achene beaks straight, 1 mm. long; leaves truncate or rounded at the bases.
The 3 primary divisions of the basal leaves once-lobed or entire; head of achenes cylindrical or ovoid-cylindrical .... 37. *R. Eschscholtzii.*
The 3 primary divisions of the basal leaves again twice-divided into linear divisions; head of achenes ovoid. (See also the varieties *Suksdorfii* and *trisectus* of *R. Eschscholtzii*) .... 38. *R. adoneus.*
Sepals densely covered dorsally with conspicuous *reddish-brown* hair.
Radical leaf blades reniform to cordate, semicircular, or nearly orbicular, palmately lobed or parted; petals obovate.
Receptacle glabrous; achene body about 1.5 mm. long ... 39. *R. nivalis.*
Receptacle brown-hispid; achene body occasionally 1.5, but ordinarily 1.8–2 mm. long .... 40. *R. sulphureus.*
Radical leaf blades very narrowly elliptic, shallowly toothed at the apices; petals cuneate; receptacle glabrous. 41. *R. Macauleyi.*
Stems not more than 5 cm. long at fruiting time (measurement to *the base of the highest pedicel*).
Petals twice as long as the sepals, 5 mm. long by 4 mm. broad ... 42. *R. Grayi.*
Petals the same length as the sepals, 1.5–3.5 mm. long by 1–2.8 mm. broad .... 43. *R. pygmaeus.*
Fruiting receptacle and head of achenes spherical or globose; achenes each with a broad thin stipe or winged base, except in *R. pygmaeus.*
Stems not more than 4 cm. long at fruiting time (measurement to the base of the highest pedicel) .... 43. *R. pygmaeus.*
Stems 5 cm. long or longer.
Herbage pilose; petals obovate-spatulate, the nectary scales glabrous; achene beaks 0.3 mm. long .... 44. *R. rhomboideus.*
Herbage glabrous; petals obovate, the nectary scales usually distally ciliate; *achene beaks 0.6 mm. long* .... 45. *R. glaberrimus.*
Horizontal rootstocks produced about 4 cm. below the surface of the soil; flowering stems scapose; head of achenes hemispherical .... 46. *R. verticillatus.*
Roots distinctly and conspicuously tuberous, the tubers truncate distally, 3–5 (rarely only 2) mm. in diameter; petals broadly oblanceolate .... 47. *R. Jovis.*

25. RANUNCULUS ABORTIVUS L. Sp. Pl. 551. 1753. *R. nitidus* Walt. Fl. Carol. 159. 1788. *R. ruderalis* Greene, Am. Midl. Nat. **3**: 334. 1914. *R. Holmei* Greene, Am. Midl. Nat. **3**: 334. 1914. *R. michiganensis* Farwell, Rept. Mich. Acad. Sci. **17**: 169. 1916. *R. abortivus* var. *typicus* Fern. Rhodora **40**: 417. 1938. *R. abortivus* var. *acrolasius* Fern. Rhodora **40**: 418. *pl. 519. f. 1–2.* 1938.

Radical leaves simple or rarely some trifoliolate, reniform, 1–5 cm. long, 1–6 cm. broad, crenulate or crenate, some 3-lobed, -parted, or -divided, petioles 4–11 cm. long, stipular leaf bases scarious, 1–2 cm. long; cauline leaves alternate, the bracts deeply once- or twice-parted to form 3 or 5 elliptic lobes, sessile; receptacle fusiform-cylindrical, about 2 mm. long in flower and 2–4 mm. long in fruit, sparsely villous.

Moist ground in rich woodland at low elevations; Juneau, Alaska, and British Columbia to Labrador, southern Colorado, eastern Texas and Chattachoochee, Florida. Northern coniferous, western pine, Northeastern pine and hardwood and Southeastern pine, and river bottom forests. March to June, depending upon locality.

Type collections: (1) *R. abortivus*, "*Habitat in* Virginia, Canada." (2) *R. nitidus.* Carolina. (3) *R. ruderalis*, "First observed by me as growing on a railway embankment near Linden station of the Baltimore & Ohio Railway, within the State of Maryland, but not far outside the District of Columbia, this in May, 1912." TYPE, *HGr. 13022–3.* (4) *R. Holmei*, "A common plant of low woodland borders and open thickets, in rich alluvial soil along the Potomac River & its tributaries in Maryland & Virginia." The following specimen is designated as a LECTOTYPE: Thicket near canal, below High Island, Maryland, *Greene*, Apr. 23, 1912, *HGr. 13027.* (5) *R. michiganensis*, "Swamp lands near Rochester, Michigan, Farwell, No. 3627, May 17, 1914." (6) Var. *acrolasius*, "Shelburne N. H., May 17, 1910, *Deane* (TYPE in Herb. N.E. Bot. Cl.). . . ." This is a northern and Rocky Mountain form with the younger portions of the plant (stems, cauline leaves, and pedicels) pubescent.

25 A. RANUNCULUS ABORTIVUS var. EUCYCLUS Fern. Rhodora **1**: 52. 1899. *R. abortivus* f. *giganteus* Gates, Trans. Kans. Acad. Sci. **33**: 28. 1930.

Stems elongated, slender and flexuous; radical leaf blades deeply cordate with a narrow basal sinus; 3.5–4.5 cm. long (on the axis), 4.5–6 cm. broad, the blade as a whole practically circular; cauline leaves like the typical species; fruiting receptacle slender.

Rich woods; Quebec to Newfoundland and south to New York and New England; Yates Center, Kansas, and Hope, Arkansas. Northern coniferous and Northeastern pine and hardwood forests. Early summer.

Specimens from Devil's Lake, North Dakota (*Lunell*, July 1, 1905, *NY.*) and from Vermont (*Carey*, *NY.*) have similar leaves but not the slender and flexuous stems.

Type collections: (1) Var. *eucyclus*, "First collected by Miss Kate Furbish at East Livermore, June, 1888." Maine. (2) F. *giganteus*, "The type specimen, 50 cm. high, collected June 5, 1928, three miles southeast of Yates Center, Kansas, deposited in the herbarium of the Kansas State Agricultural College, Manhattan, Kansas, by Mrs. C. E. Rogers" (O. E. Rogers on the label). The specimen was kindly loaned to the University of Arizona by Dr. F. C. Gates. The fruiting receptacle is of a nearly filiform type rarely equalled in narrowness in the typical species or the var. *eucyclus*, and the radical leaves are 4.5–6 cm. long (on the axis), or 8–9 cm. if the basal lobes are included. The basal sinus is about 3 cm. deep. The flowers are unknown. This form is truly remarkable for its size, but it is deficient in technical characters to differentiate it as a variety.

25 B. **Ranunculus abortivus** var. **indivisus** Fern. Rhodora **40**: 418. *Pl. 518*. 1938.

Herbage a darker green than in the typical species; stems like the typical species; radical leaf blades shaped like those of the typical species, but the teeth very shallow; bracts cuneate, obovate, apically shallowly-lobed or -toothed.

Alluvial woods of bottom-land; Nottaway River Valley, Southhampton County, Southeastern Virginia. River Bottom Forest. April.

Type collection: "Three Creek, Drewryville, April 9, 1938, *Fernald & Long*, No. 7829 (TYPE in Gray Herb., ISOTYPE in Herb. Phil. Acad.). . . ."

26. **Ranunculus micranthus** Nutt. ex Torr. and Gray, Fl. N. Am. **1**: 18. 1838. *R. delitescens* Greene, Am. Midl. Nat. **3**: 333. 1914. *R. cymbalistes* Greene, Am. Midl. Nat. **3**: 333. 1914. *R. micranthus* var. *delitescens* Fern. Rhodora **41**: 543. 1939. *R. micranthus* var. *cymbalistes* Fern. Rhodora **41**: 543. 1939.

Low elevations; South Dakota to Arkansas and thence to southern Illinois, southern Indiana, and Kentucky; Massachusetts to the District of Columbia. April or May.

Type collections: (1) *R. micranthus*, " 'Margins of ponds throughout the upper & western part of Missouri, likewise in Arkansas, collected by *Dr. Pitcher.' Nuttall!*" The Pitcher specimen in the New York Botanical Garden is designated as a LECTOTYPE. It was collected at Ft. Gratiot (?). (2) *R. delitescens.* "Guttenberg, New Jersey, 12 May, 1895, by William Van Sickle. . . . Harper's Ferry, W. Va., 11 May, 1889, by F. V. Coville." (3) *R. cymbalistes*, "Known only as collected in extreme southern Indiana, 20 April, 1913, by Mr. Charles C. Deam, where it inhabits wooded knolls, under Pinus Virginiana & Quercus alba, the special locality 2 miles west of New Albany."

27. **Ranunculus allegheniensis** Britt. Bull. Torrey Club **22**: 224. 1895.

Moist woodland in New England (uncommon and not found in Maine) and in the mountains from Franklin County, Pennsylvania, to Waynesville, North Carolina. Northeastern pine and hardwood forests. May or early June.

Type collection: "Mountains of Virginia & North Carolina." The following specimen is designated as a LECTOTYPE, White Top Mountain, Grayson County, Virginia, *N. L. & E. G. Britton and A. M. Vail* in 1892, *NY*.

28. **Ranunculus Harveyi** (A. Gray) Britt. Mem. Torrey Club **5**: 159. 1894. *R. abortivus* L. var. *Harveyi* A. Gray, Proc. Am. Acad. **21**: 372. 1886. *R. Harveyi* Greene, Erythea **2**: 189. Dec. 1, 1894. *R. Harveyi* var. *pilosus* Benke, Rhodora **30**: 200. 1928.

Moist woodland; Southern Missouri and Arkansas; vicinity of Tuscaloosa, Alabama (e.g., *Harper 3181, NY.*). Southern hardwood and river bottom forests. Late April and early May.

Type collections: (1) Var. *Harveyi*, "On damp rocks in Arkansas, *F. L. Harvey* and *Dr. Hass* [Hasse]." (2) Var. *pilosus*, "The type is from Rolla, Mo., Apr. 18, 1928, H. C. Benke 4575 in Field Museum."

29. RANUNCULUS ARIZONICUS Lemmon. A. Gray, Proc. Am. Acad. **21**: 370. 1886. *R. nudatus* Greene, Leafl. Bot. Obs. & Crit. **1**: 211. 1906.

Dry situations at 1,600–2,250 meters elevation; Greenlee and Santa Cruz Counties, Arizona, to Santa Rita, New Mexico. Western pine forest (?), southwestern coniferous woodland, and oak woodland. Flowering in the summer rainy season.

Type collections: (1) *R. arizonicus*, "Lemmon, in herb. Gray. . . . The plant sent by Mr. Lemmon with this name is the same as C. Wright's no. 837, also from Arizona, and which was taken for a form of *R. affinis* in the Botany of the Mexican Boundary." The Lemmon specimen is the type. It was collected in Rucker Valley, Chiricahua Mountains, Sept. 28, 1881, *Lemmon 585*. (2) *R. nudatus*, "Burro Mountains, at 7,500 feet, O. B. Metcalfe, 20 June, 1903." The TYPE is *HGr. 2815*.

30. RANUNCULUS CARDIOPHYLLUS Hook. Fl. Bor. Am. **1**: 14. *pl. 5. f. B.* 1829. *R. affinis* R. Br. var. *cardiophyllus* A. Gray, Proc. Acad. Phila. **15**: 56. 1864. *R. affinis* R. Br. var. *lasiocarpus* Torr. Bot. Wilkes Exped. **17**: 213. 1874. *R. affinis* var. *validus* A. Gray, Proc. Am. Acad. **21**: 371. 1886. *R. cardiophyllus* var. *pinetorum* Greene, Pittonia **4**: 144. 1900. *R. pedatifidus* J. E. Smith var. *pinetorum* Davis, Minn. Bot. Studies **2**: 483. 1900. *R. affinis lasiococcus* Torr. ex Piper, Contr. U. S. Nat. Herb. **11**: 273. 1906, as syn.

Stems erect, not rooting adventitiously, 2–4 dm. long and 2–4 mm. in diameter, 1–5-, or 8-flowered, fistulous, pilose, striate; radical leaf blades simple, cordate, 1–6 cm. long, 1–5 cm. broad, crenate, sometimes the apex lobed or rarely parted, proximally cordate and distally rounded, pilose, petioles 5–10 or 16 cm. long, pilose, stipular leaf bases 2–4 cm. long, not markedly fibrous after withering; cauline leaves alternate, the bracts divided into 3–7 linear lobes, sessile; petals 5, yellow, broadly cuneate-obovate, 8–15 mm. long, 6–13 mm. broad, the nectary scale ciliate on its apical margin with hairs nearly 1 mm. long (the surrounding petal surface often with similar hairs), forming a pocket, obdeltoid; achenes 50–125 in a cylindrical head 8–10 or usually 10–15 mm. long by 5–6 or usually 7–9 mm. in diameter, each achene obovate, 2 mm. long, 1.5 mm. dorsoventrally, 0.6–0.8 mm. laterally, smooth, finely canescent, margin inconspicuous, the achene beak slender, 0.6–1 mm. long, recurved; receptacle ovoid-cylindrical, 3–4 mm. long in flower, 7–14 mm. long in fruit, densely hairy.

Meadows in the mountains at 2,500–3,350 meters elevation southward and at 600–1,500 meters northward; Moose Mountain, Northwest Territory; Rocky Mountain system in Alberta and from Wyoming and the Black Hills to Northern Arizona and the northern edge of New Mexico. Western pine forest. Mostly July.

Type collections: (1) *R. cardiophyllus*, "Hab. from Canada to lat. 55°. In the central prairie & limestone districts. *Dr. Richardson. Drummond.* Alpine prairies in the Rocky Mountains. *Drummond.*" (2) Var. *lasiocarpus*, "Columbia River between the Spokane and Fort Colville." *Wilkes Expedition.* (3) Var. *validus*, "Taking the slender, high-northern form with even the leaves sometimes 'pedately multifid,' as the original of the species, the above name may be given generally to the stouter and larger forms, of lower altitudes or elevations, with more succulent leaves, . . . to this belongs *R. cardiophyllus*, Hook., figured both in the Fl. Bor.-Am. & in Bot. Mag. t. 2999 but with the style too long.'' This name is considered to be a new one for *R. cardiophyllus* and to be based upon the same type. (4) Var. *pinctorum*, '' 'Abundant in pine woods, at Graham's Park, 7,800 ft.' southern Colorado, 12 May, 1899, C. F. Baker.'' The TYPE is *HGr. 2547*. (5) *R. affinis lasiococcus*. *Lasiococcus* apparently unintentionally substituted for *lasiocarpus*.

30 A. RANUNCULUS CARDIOPHYLLUS var. SUBSAGITTATUS (A. Gray) L. Benson, Am. Jour. Bot. **27**: 187. 1940. *R. arizonicus* Lemmon var. *subsagittatus* A. Gray, Proc. Am. Acad. **21**: 370. 1886. *R. subsagittatus* Greene, Pittonia **2**: 59. 1890.

Stems scapose, 1–1.5 or 2.5 mm. in diameter, usually unbranched below, 1–3- or 4-flowered, a little fistulous, glabrous or pilose; radical leaf blades simple, cordate or long-ovate or rarely subsagittate, 1.5–4.5 cm. long, 1–4 cm. broad, crenately toothed, proximally cordate (often deeply so) or rounded and distally rounded or obtuse or acute, petioles pilose or glabrous, stipular leaf bases 1–2 cm. long; cauline leaves all bracts, consisting of 1–5 linear divisions; petals 5, yellow, glossy on only the distal part, obovate or obovate-obdeltoid, sometimes deeply emarginate, 7–15 mm. long, 5.5–13 mm. broad, the nectary scale oblong; achenes mostly 20–50 in an ovoid head usually 5–6 mm. long by 4–6 mm. in diameter, the achene beak slender, straight; receptacle ovoid, 1–2 mm. long in flower and 4–7 mm. long in fruit.

Mountain meadows and stream banks at 2,300 to 3,000 meters elevation; east-central Arizona and west-central New Mexico. Mostly Western pine forest. July and August.

Type collection: ''North Arizona in De La Vergne Park of the San Francisco Mountains, in wet ground, Lemmon.'' Aug., 1884.

30 B. RANUNCULUS CARDIOPHYLLUS Hook. var. COLORADENSIS L. Benson, Am. Jour. Bot. **27**: 804. *pl. 1. f. 7.* 1940.

Radical and lower cauline leaves ovate, the bases acute or obtuse, shallowly crenately-toothed; petioles of the radical leaves 8–18 cm. long; petals oblanceolate-obovate, 5–10 mm. long; otherwise like the typical species.

Mountain meadows at 2,800 meters elevation; Silverton, Colorado. Northern coniferous forest. July.

Type collection: ''Silverton, Colorado, 9,500 elevation, *Herbarium of the State Agricultural College of Colorado* (collector not designated), July 3, 1898. Type in the New York Botanical Garden.'' An isotype from the Colorado State College Herbarium has been examined.

31. RANUNCULUS EASTWOODIANUS L. Benson, Am. Jour. Bot. **27**: 804. *pl. 1. f. 13.* 1940.

Known only from the type collection at Skagway, Alaska. Northwestern coniferous forest.

Closely allied to *R. pedatifidus* J. E. Smith. The species is named for Miss Alice Eastwood, Curator of the Herbarium of the California Academy of Sciences.

Type collection: "Skagway, Alaska, *Louise Huffine*, summer 1925, *California Academy of Sciences 138,383.*"

32. RANUNCULUS PEDATIFIDUS J. E. Smith in Rees. Cyclop. **29**: *R.* sp. No. 72. 1819. *R. affinis* R. Br. Bot. App. Parry's 1st Voy. 265. 1824. *R. affinis* var. *leiocarpa* Trautv. Middendorff's Reise **1**: 62. 1847. *R. vicinalis* Greene, Pittonia **4**: 145. 1900. *R. apetalus* Farr, Ottawa Nat. **20**: 110. 1906. *R. pedatifidus* var. *leiocarpus* Fern. Rhodora **19**: 138. 1917.

Meadows in the Rocky Mountains at 2,800–3,500 meters in Colorado and at 800–1,500 meters in Alberta and tundra at low elevations on the arctic plains; Northern Asia; Yukon to Baffin Island, Labrador, and Greenland and southward to Alberta and Saskatchewan; Wyoming (Albany County) and Colorado. Arctic-Alpine grassland and northern coniferous forest. June and July.

An apetalous form occurs in the Rocky Mountains from the Athabasca River to Banff and in Gilpin County, Colorado. It was collected also by Hall and Harbour in Colorado in 1862 (*U.S.*).

Type collections: (1) *R. pedatifidus*, "Native of Siberia. Four specimens from that country are in the Linnaean herbarium. . . ." (2) *R. affinis*, "Collected in Melville Island, By the officers of the Expedition." "Chiefly in the vicinity of Winter Harbour . . . herbaria of Captain Sabine, Mr. Edwards, Mr. James Ross, Captain Parry, Mr. Fisher, & Mr. Beverly." (3) Var. *leiocarpa*, "In speciminibus taimyrensibus omnibus Ranunculi affinis R. Br. ovaria prorsus glabra sunt. . . ." Fernald's application of this varietal epithet was to a glabrous-fruited population best-developed in eastern Arctic America. Cf. also Fernald, Rhodora **36**: 93–96, 97. pl. 279–80. 1934. (4) *R. vicinalis*, "At Fort Selkirk on the Yukon River, in dry gravelly soil, 9 June, 1899, M. W. Gorman." (5) *R. apetalus*, "By the roadsides at Banff, Alberta."

A form collected on Mt. San Francisco, Arizona (*Little 4632*, *Sac*), and on loose calcareous slopes near snow banks at 11,800 feet on the northeast side of Delano Peak in the Tushar Range in Piute County, Utah (*Maguire 19278*, Herbarium of Utah State College) may be a new variety. It has the following characters: stems 4–15 cm. long; radical leaf blades 1–2 cm. long, deeply lobed or cleft into simple lobes, the upper lobes erect, the lower markedly divergent or somewhat reflexed; petals none.

33. RANUNCULUS SABINII R. Br. App. Parry's 1st. Voy. 264. 1824.

Wet ground in arctic regions; Melville Island to Ellesmere Land and northwestern Greenland. Arctic-alpine grassland. July and August.

Type collection: "Collected in Melville Island, By the Officers of the Expedition." "Chiefly in the vicinity of Winter Harbour. . . ." "Planta inter R. nivalem et Pygmaeum media in Herb. *D. Sabine* extat."

34. RANUNCULUS INAMOENUS Greene, Pittonia **3**: 91. 1896. *R. affinis* R. Br. var. *micropetalus* Greene, Pittonia **2**: 110. 1890. *R. micropetalus* Rydb. Bull. Torrey Club **29**: 158. 1902.

Hirsute to subglabrous terrestrial perennials; radical leaf blades simple and ovate, obovate, or orbicular, 1–4 cm. long, 1–3.5 cm. broad, at least some radical leaves on each plant crenate, rarely some 3-lobed or -divided, proximally more or less attenuate and distally rounded, glabrous or appressed-pubescent, petioles 4–10 cm. long, appressed-pubescent, stipular leaf bases 1.5–2.5 or rarely 4 cm. long; cauline leaves alternate, the bracts of 3–5 nearly linear lobes, sessile; pedicels 3–10 mm. long in flower and 10–50 or rarely 70 mm. long in fruit, appressed-pubescent; sepals narrowly obovate, 3–5 mm. long, about 2–2.5 mm. broad; petals narrowly elliptic to obovate, 2.5–8 mm. long, 2–4 mm. broad; achenes 60–100 in a cylindric or barrel-shaped head 7–17 mm. long by 6–8 mm. in diameter, each achene nearly obovate, about 1.5 mm. long, 1.3 mm. dorsoventrally, 0.5–0.6 mm. broad laterally, smooth, densely short-pubescent, margin inconspicuous, the achene beak slender, 0.8–0.9 mm. long, recurved; receptacle slender and cylindric, 2–3 mm. long in flower and 6–15 mm. long in fruit, hispid.

Moist ground in the mountains at 2,000 to 3,000 meters elevation; Rocky Mountain System from Alberta to Mt. San Francisco, Arizona and the Sacramento Mountains, New Mexico; in Idaho collected in only Custer County. Western pine (lodgepole pine) forest. Mostly June and July.

Type collections: (1) Var. *micropetalus*, "*R. Arizonicus*, var. *subaffinis* Greene," Pittonia **2**: 60. 1890, "not of Gray," Proc. Am. Acad. **21**: 370. 1886. "On the San Francisco Mountain (which some recent explorers and visitors effect to call Mt. Agassiz) it grows along cold subalpine brooklets where it is associated with *Mertensia Siberica*, *Primula Parryi*, etc." Greene's collection from Mt. San Francisco in 1889 is designated as a LECTOTYPE. It is *HGr 1198*. The petals of the type specimen are 4–5 mm. long. The short-petalled and small-fruited form, which includes practically every specimen from Utah, Arizona, and New Mexico, most of those from the northern Rocky Mountains, and many from Colorado might be recognized as a variety based upon *R. affinis* var. *micropetalus*. However, gradual intergradation is found in both characters, and it seems better to consider *R. inamoenus* as variable in size of flowers and fruit, even though small petals and small fruit commonly accompany one another, and the two characters are found together through a large but indefinite geographical range. (2) *R. inamoenus*, "Common in the whole Rocky Mountain Region, at middle elevations, and hitherto erroneously treated as a variety of the arctic *R. affinis*." That in 1890 Greene considered the central and northern Rocky Mountain plant somewhat different from his variety *micropetalus* on Mt. San Francisco, Arizona, is shown by the following statement, Pittonia **2**: 110. 1890, "It [var. *micropetalus*] differs from the Colorado and northern *R. affinis* only in its much more slender habit, minute flowers, and long cylindrical head of achenes." Since there is no recorded change of opinion between 1890 and 1896, it may be assumed that the variety *micropetalus* is not the "variety of the arctic *R. affinis*" mentioned by Greene in 1896 and that the species *inamoenus* was based upon a different type. This viewpoin was taken by Rydberg, Fl. Colo. 145. 1906. Coulter, Man. Rocky Mt. Bot. 8 1885, recognized two varieties of *R. affinis* for the Rocky Mountains. One was based upon *R. cardiophyllus* Hook. (*R. affinis* var. *cardiophyllus* A. Gray, Proc. Acad. Phila. **15**: 56. 1864, which has now a later typonym, *R. affinis* var. *validus* A. Gray, Proc. Am. Acad. **21**: 371. 1886.) Since the variety *cardiophyllus* of Coulter's Manual is described as having "*flowers an* *inch in diameter,"* it could not have been the type of *R. inamoenus* with the whole "corolla 3–5 lines broad." The other variety was identified by Coulter as *R. affinis* var. *leiocarpus* Trautv. and described as having small flowers, and it is probable that Greene had this variety in mind when he described *R. inamoenus*, although the proof is not necessarily adequate. Since Greene gave no type and only a vague reference to a variety of *R. affinis*, it is necessary to establish the identity of the species *inamoenus* by reference to the Herbarium Greeneanum, which contains 15 or 20 specimens. The following were collected by Dr. Greene prior to publication of the species, Nov. 9, 1896: Upper Bear Creek, Colorado, *Greene* in 1889; Dale Creek, Wyoming, *Greene* June 30, 1896. The writer designates the Dale Creek specimen, *H. Gr. 2639* and *2648*, as a Lectotype.

Significant specimens: Idaho: Bonanza, Custer County, *Macbride & Payson 3471, NY;* Cape Horn, Custer County, *Macbride & Payson 3621, NY.* Colorado: (all with fruit larger than usual, 2 mm. long): Eldora to Baltimore, Gilpin County, *Tweedy 5688, NY;* Berthoud Pass, 11,000 feet, *Tweedy 5689, NY* (achene beaks nearly straight); Cuchara River above La Veta, 2,100 meters, *Rydberg & Vreeland 6244, NY.*

34 A. Ranunculus inamoenus var. **alpeophilus** (A. Nels.) L. Benson, comb. nov. *R. alpeophilus* A. Nels. Bull. Torrey Club **26**: 350. 1899. *R. utahensis* Rydb. Bull. Torrey Club **29**: 158. 1902. *R. inamoenus* var. *alpeophilus* L. Benson in Abrams, Ill. Fl. Pac. Sts. **2**: (perhaps appearing in advance of this paper).

Herbage practically glabrous; radical leaf blades 3-parted or some of them 3-lobed; achenes and usually the receptacle glabrous; otherwise like the typical species.

Moist slopes in the mountains at mostly 2,500 to 3,000 meters elevation; Yoho Valley, British Columbia; Wyoming and the East Humboldt (Ruby) Mountains, Nevada to Utah and Central Colorado. Western pine forest (mostly lodge pole pine). Summer.

Type collections: (1) "Several collections of it have been secured, from nearly alpine stations in the State of Wyoming, growing in moist, rich soil. Nos. 1780 and 4211 by the writer, and no. 5252 by Mr. Elias Nelson may be cited as typical." The type is established by the following excerpt from a letter received from Dr. Aven Nelson and dated December 21, 1938: "Replying to your valued inquiry concerning *Ranunculus alpeophilus*, I will state that my number which I have designated as type and which I find in our type case is 4211, Battle Creek Mountain, August 17, 1897, collected by myself." (2) *R. utahensis*, "Utah: Alta, Wasatch Mts., 1879, *M. E. Jones, 1130.* (Type in herb. Columbia University.)" This is a form with thick leaves and robust stems.

34 B. Ranunculus inamoenus var. subaffinis (A. Gray) L. Benson, Am. Jour. Bot. **27**: 187. 1940. *R. arizonicus* Lemmon var. *subaffinis* A. Gray, Proc. Am. Acad. **21**: 370. 1886. *R. subsagittatus* (A. Gray) Greene var. *subaffinis* Greene, Pittonia **2**: 110. 1890. *R. subaffinis* Rydb. Bull. Torrey Club **24**: 246. 1897.

Stipular leaf bases 2.5–3 cm. long; pedicels 10–33 mm. long in flower and 60–80 mm. long in fruit; sepals obovate, 5–7 mm. long, 3.5–4.5 mm. broad;

petals mostly obovate or obovate-lanceolate, 6–9 mm. long, 2.5–7 mm. broad; achenes about 50–60 in an ovoid or cylindric head 6–11 mm. long by 5–7 mm. in diameter, each achene about 2–2.3 mm. long, 1.5–1.7 mm. dorsoventrally, the beak about 1.5–2 mm. long, straight (or bent or curved out of position in herbarium specimens), the margin a little more conspicuous than in the typical species or some achenes showing evidence of a very broad margin.

Moist ground near timber line at about 3,400 meters elevation; Mt. San Francisco, Arizona. Northern coniferous forest. June and July.

Type collection: "Mt. Agassiz [Mt. San Francisco], *Lemmon.*" *4152*, collected near the summit at 12,000 feet elevation, September, 1884.

Significant specimens. Arizona: Mt. San Francisco, *Greene*, in 1889, *HGr, NY, Mearns* in 1887, *NY;* San Francisco Peaks, margin of the crater, 10,300 feet, *L. Benson 9628, B, UA;* San Francisco Peaks, *Whiting & Sanders* in 1935, *UA;* Near Flagstaff, *P. L.* in 1928, *UA*, Mt. San Francisco, *Little 4697, Sac.*

35. Ranunculus Allenii Rob. Rhodora **7**: 220. 1905.

Meadows at 950–1300 meters (or lower northward); Akpatok Island and the Labrador Peninsula Labrador to Gaspe County, Quebec. Arctic-alpine grassland and northern coniferous forest. July and August.

Type collection: "Gaspe County, Quebec: on flood plain of an alpine Brook, north face of Mt. Albert, alt. 770 to 1100 m., 14 August, 1905. *J. F. Collins* & *M. L. Fernald*, no. 83. (Type, in herb. Gray.)"

36. Ranunculus verecundus Rob. *R. verecundus* Rob. apud Piper, Contr. U. S. Nat. Herb. **11**: 274. 1906. *R. ramulosus* Jones, Contr. W. Bot. **14**: 47. 1912.

Wet slopes near timber line from near sea level (northward) to 3,000 meters elevation (southward); rare but widely distributed; Russell Fiord, Central Alaska; Sawback Mountain, Alberta; Mt. Stuart and Mt. Adams, Washington; Strawberry Mountains, Oregon; Woolly Creek, Siskiyou County, California (?); Custer and Blaine Counties, Idaho; Long Baldy, Little Belt Mountains and Glacier National Park, Montana. Arctic-alpine grassland. July and August.

Type collections: (1) *R. verecundus*, "Wet, gravelly places, Mt. Paddo [Adams], alt. 1850–2150 meters, July 31, 1883, *W. N. Suksdorf 93.* (Type in Hb. Gray.)" (2) *R. ramulosus*, "Swift Current Pass, Glacier National Park, 7,000 feet, *M. E. Jones* August 11, 1910." Herbarium of Pomona College.

Significant specimens. Alaska, Washington, Oregon, California, and Idaho, cf. L. Benson, Am. Jour. Bot. **23**: 170. 1936. Alberta: Sawback Mountain, *Sanson 140, NY*. Montana: Long Baldy, Little Belt Mountains, *Flodman 469, NY;* Mineral Park, Glacier National Park, 7,000 feet, *Jones* in 1910, *P;* Swift Current Pass, Glacier National Park, 7,000 feet, *Jones* in 1910, *P;* Sexton Glacier, *Standley 17230, US.*

37. Ranunculus Eschscholtzii Schlect. Animad. Ranunc. **2**: 16. *pl. 1.* 1820. *R. nivalis* L. var. *Eschscholtzii* S. Wats. King's Rept. **5**: 8. 1871.

R. ocreatus Greene, Pittonia **4**: 15. 1899. *R. Helleri* Rydb. Bull. Torrey Club **29**: 158. 1902. *R. Eschscholtzii* var. *Helleri* L. Benson, Am. Jour. Bot. **23**: 169. 1936.

Caudex 1–2 cm. long, 3–6 mm. in diameter; radical leaf blades simple, semi-circular to reniform, 1.3–3 cm. long, 2.5–4 cm. broad, deeply 3-parted, the middle lobe again 3-lobed or entire, the lateral asymmetrically 3–7-parted, the ultimate lobes and sinuses rounded, the blade proximally truncate or rounded, petioles 2–8 cm. long, stipular leaf bases 1–1.5 cm. long, annually deciduous or disintegrating; petals 5 or usually 7–10 mm. long, 5–10 mm. broad; achenes glabrous.

Boreal and Alpine meadows and talus slopes from the Aleutian Islands and coastal Alaska to Crater Lake and scattering stations in the central Sierra Nevada, California, to the Wallowa Mountains in Eastern Oregon, to the East Humboldt or Ruby Mountains in Nevada, and to Alberta, Utah, and Colorado; Mt. San Francisco, Arizona; possibly New Mexico. Arctic-Alpine grassland. July and August.

The form south of the Canadian boundary has commonly an entire and lingulate middle leaf lobe (previously described as var. *Helleri*). A Utah and Colorado form has the stipular leaf bases often 1.5–2.5 cm. long (*R. ocreatus* Greene).

Type collections: (1) *R. Eschscholtzii*, "Hab. in insulis Unalascha et St. Georgii (de Chamisso)." (2) *R. ocreatus*, "Collected by Baker, Earle, & Tracy on Mt. Hesperus, Colorado, 2 July, 1898 (n. 912)." The TYPE is *HGr. 2740.* (3) *R. Helleri*, "IDAHO: near Lake Pend d'Oreille, 1892, *Sandberg, MacDougal, & Heller 842* (type in N. Y. Bot. Gard.)." The type has not been located at the New York Botanical Garden, but an ISOTYPE is in the Dudley Herbarium at Stanford University.

Significant specimens of *R. Eschscholtzii* and its Pacific States varieties, cf. L. Benson, Am. Jour. Bot. **23**: 169–170. 1936; also CALIFORNIA: Piute Mt., Sierra Nevada, *Jepson 4579 J;* Mt. Dana, Yosemite National Park, *M. S. Baker 4293 b* (Santa Rosa Junior College Herb.) and a few other collections from the central Sierra Nevada.

KEY TO THE VARIETIES

Ultimate basal leaf lobes and sinuses usually sharply acute, rarely obtuse in var. *eximius*.
  Basal leaf blade deeply parted, the middle lobe again 3-lobed ...... 37A. var. *Suksdorfii*.
  Basal leaf blade cleft, rarely parted, the middle lobe entire .... 37B. var. *eximius*.
Ultimate basal leaf lobes rounded or obtuse, at least not sharply acute.
  Caudex 1–2 cm. long, unbranched; scarious or thickened stipular leaf bases 1–2 cm. long, deciduous or disintegrating annually; achenes glabrous .... 37. *R. Eschscholtzii*.
  Caudex 1.5 or 3–7 cm. long, often branched; thickened stipular leaf bases 1.5–3 cm. long, usually persistent for 2 or more seasons.
    Middle basal leaf lobe again 3- to 7-lobed; achenes pubescent or glabrous; leaves deeply parted .... 37C. var. *trisectus*.
    Middle basal leaf lobe entire, or very rarely 3 lobed; achenes glabrous; leaves usually cleft, rarely parted .... 37D. var. *oxynotus*.

37 A. RANUNCULUS ESCHSCHOLTZII var. SUKSDORFII (A. Gray) L. Benson, Am. Jour. Bot. **23**: 170. 1936. *R. Suksdorfii* A. Gray, Proc. Am. Acad. **21**: 371. 1886.

Caudex 1–1.5 or rarely 2.5 cm. long, 3–5 or 7 mm. in diameter; radical leaf blades thin, deeply 3-parted, the middle lobe again 3-lobed, the ultimate lobes and sinuses sharply acute, scarious stipular leaf bases 1–2 cm. long, annually deciduous or disintegrating; petals 7–11 mm. long, 5–10 mm. broad; achenes glabrous.

Mountain meadows and slopes at 1,700–2,000 meters elevation; Washington in the Olympic and Cascade Mountains; Idaho; Western Montana; Northwestern Wyoming. Arctic-Alpine grassland. July and August.

Plants from Idaho, especially the southern part, and from Wyoming are intermediates between var. *Suksdorfii* and *Ranunculus adoneus* A. Gray var. *alpinus* (S. Wats.) L. Benson.

Type collection: "Mt. Adams, Washington Terr., at 6,000 to 7,000 feet, in damp ground, *Suksdorf*," 1884.

37 B. RANUNCULUS ESCHSCHOLTZII var. **eximius** (Greene) L. Benson, comb. nov. *R. eximius* Greene, *Erythea* **3**: 19. 1895. *R. saxicola* Rydb. Mem. N. Y. Bot. Gard. **1**: 64. 1900.

Caudex 1–2 cm. long, 3–7 mm. in diameter; basal leaves usually thin, cleft or rarely parted, the middle lobe entire, the ultimate lobes and sinuses sharply acute, or rarely somewhat obtuse, scarious stipular leaf bases 1–2 or 2.5 cm. long, annually deciduous or disintegrating; petals 8–12 or sometimes 17 mm. long, 6–11 or 19 mm. broad; achenes glabrous or rarely hairy.

Alpine meadows at 2,300–3,000 meters; mountains of Western Montana and Northwestern Wyoming; Big Horn Mountains and Battle, Carbon County, Wyoming (*Tweedy* in 1901); Fremont County, Idaho; La Sal Mountains, Southeastern Utah; Mt. San Francisco, Arizona. Arctic-Alpine grassland. July and early August.

This variety is related to *R. adoneus*.

Type collections: (1) *R. eximius*, "A most beautiful alpine and subalpine species of the Rocky Mountains in Colorado, Wyoming, and Idaho, apparently somewhat rare, but gathered sparingly, and in poor specimens even by Hall and Harbour, in whose collection it is mixed with *R. adoneus* as far as distributed. Better specimens have been obtained by Mr. Buffum of Laramie." The following specimen is designated as a LECTOTYPE: Little Bald Mountains, *B. C. Buffum* in 1892, *HGr 2592.* (2) *R. saxicola*, "MONTANA: Cedar Mountain, July 16, 1897, *Rydberg & Bessey, 4112* and *4113;* Mill Creek, 1887, *Tweedy 192.* YELLOWSTONE PARK: Electric Peak, August 18, 1897, *Rydberg & Bessey 4111;* 1895, *Tweedy, 192;* Mt. Holmes, 1884, *Tweedy, 301.*" *No. 4112* of *Rydberg & Bessey* from Cedar Mountain, Montana is designated as a LECTOTYPE. It is in the New York Botanical Garden.

Significant specimen. ARIZONA: Mt. San Francisco, 10,500 ft., *Whiting & Sanders* Cat. No. 756/1060, Museum of Northern Arizona Herbarium.

37 C. RANUNCULUS ESCHSCHOLTZII var. TRISECTUS (Eastw.) L. Benson, Am. Jour. Bot. **23**: 170. 1936. *R. trisectus* Eastw. apud Rob. Proc. Am. Acad. **45**: 394. 1910.

Caudex 1 or 3–6 cm. long, 4–7 mm. in diameter, usually branched; basal leaves usually thin, deeply 3-parted, the middle lobe again 3- to 7-lobed, scarious stipular leaf bases 1.5–2.5 cm. long, usually persistent for a season or more after death of the leaf; achenes hispid or glabrous.

Mountain slopes and meadows at 2,000–3,000 meters elevation; Yoho River, British Columbia and Spray River, Alberta; Wallowa, Strawberry, and Steen Mountains, Eastern Oregon; Payette Lake, Idaho; Black Rock Creek, Teton National Forest, Wyoming. Arctic-Alpine grassland. Mostly July.

Closely related to *Ranunculus adoneus.*

Type collection: "Alpine Wallowa Mountains, Eastern Oregon, Altitude 2745 m., growing at the base of cliffs, *William C. Cusick* No. 3200."

37 D. RANUNCULUS ESCHSCHOLTZII var. OXYNOTUS (A. Gray) Jepson, Fl. Calif. 1: 537. 1922. *R. oxynotus* A. Gray, Proc. Am. Acad. **10**: 68. 1875.

Caudex 3–7 mm. long, 5–12 mm. in diameter, often branched; basal leaves thick, cleft or rarely parted, the middle lobe entire and lingulate or rarely (Tulare County) 3-lobed, the 2 lateral lobes crenate, stipular leaf bases thick and persistent for one or more seasons; achenes glabrous.

Mountain meadows and talus slopes at 3,000–3,850 meters; California in the Warner Mountains, in the Sierra Nevada from Mt. Stanford (Castle Peak), Sierra County to Tulare County, in the White Mountains of Inyo County, and in the San Bernardino and San Jacinto Mountains. Arctic-Alpine grassland. Mostly July.

Type collection: "California, near the summit of Castle Peak [Mt. Sanford], Sierra County, at 9,000 feet, J. G. Lemmon."

38. RANUNCULUS ADONEUS A. Gray. Proc. Acad. Phila. **15**: 56. 1864.

Caudices 3–4 cm. long and 4–10 mm. in diameter, often as many as 9 in a cluster, closely and densely clothed with dead leaf bases; radical leaf blades finely divided, semi-circular to reniform in outline, 1–2 cm. long, 2–3 cm. broad, deeply parted, the primary divisions again twice-lobed into linear segments, proximally truncate or cordate and distally rounded, petioles 4–10 cm. long, stipular leaf bases 3–4 cm. long, persisting one or more seasons; cauline leaves alternate, about 2, the bracts dissected, sessile; petals when fully expanded 13–18 mm. long, 10–19 mm. broad; achene beak filiform, 1.2–1.5 mm. long, falcate-curving and often recurved.

Moist ground above timber line at 3,000–4,000 meters elevation; Northwestern Wyoming; occasional in the Wasatch and Uintah Mountains, Utah; Colorado. Arctic-alpine grassland. July and August.

Type collection: "No. 81 of last year's collection by Dr. Parry." Rocky Mountains in Colorado Territory, 1862.

38 A. RANUNCULUS ADONEUS var. **alpinus** (S. Wats.) L. Benson, comb. nov. *R. orthorhynchus* Hook. var. *alpinus* S. Wats. in King's Rep't. **5**: 9. 1871. *R. stenolobus* Rydb. Bull. Torrey Club **29**: 159. 1902.

Caudex 2–3.5 cm. long, flowering stems 15–30 cm. long, more branched than in the typical species; ultimate leaf divisions 1–2 mm. broad, the stipular leaf base more frequently scarious than thick, 2–3.5 cm. long; petals when fully expanded 8–13 mm. long; achene beaks usually not recurved.

Near snow banks at 3000–3500 meters elevation; northwestern Wyoming and the Wasatch and Uintah Mountains, Utah. Arctic-alpine grassland. July and August.

Numerous Idaho and western Wyoming specimens connect this variety with *R. Eschscholtzii* var. *Suksdorfii*.

Type collections: (1) Var. *alpinus*, "The large form occurs in low lands in Washington Territory; the variety, in the Wahsatch Mountains, at an altitude of 10,000 feet; July." The TYPE is Wasatch Mountains, Utah, 40th Parallel, 10,000 (9,000 on some labels) feet, *S. Watson* in July, 1869. Confused with *R. orthorhynchus* probably because of the dissected leaves. (2) *R. stenolobus*, "WYOMING: Headwaters of Cliff Creek, 1900, *C. C. Curtis* (type in herb. N. Y. Bot. Gard.)."

39. RANUNCULUS NIVALIS L. Sp. Pl. 553. 1753. *R. nivalis* f. *subglobosus* Polunin, Bull. Nat. Mus. Can. (92) pt. 1: 215, *pl. 6. f.* (*b*), *upper left*. 1940.

Boggy tundra mostly near sea level or up to 800 meters elevation near Mt. McKinley, Alaska; circumboreal; Northern Alaska and along the shore and islands of the Arctic Ocean to Labrador; Greenland and Iceland. Arctic-alpine grassland and tundra. July and August.

A specimen from Capitol Peak, Colorado (*Penland 1512, CA*) is probably this species. According to Dr. Penland, none of the specimens have fruit. The glabrous receptacle agrees with *R. nivalis*. The plant shows some resemblance to *R. adoneus*, however.

Type collections: (1) *R. nivalis*, "*Habitat in alpibus Lapponiae, Helvetiae.*" The following statement appears in Rees' Cyclopedia, volume 29 (pages not numbered; *Ranunculus* under "R"), "Found by Linnaeus in Lapland, by the alpine rivulets on the snowy mountains of that country. Martens had previously gathered it in Spitzbergen." (2) f. *subglobosus*, "Type in the British Museum: *Nicholas Polunin*, Wohlstenholme, Hudson Strait, No. 233, August 27, 1934."

40. RANUNCULUS SULPHUREUS Phipps, Voy. N. Pole 202. 1774. *R. altaicus* Laxm. Nov. Comm. Acad. Petrop. **18**: 533. 1774.

Tundra near sea level; circumboreal; Bering Straight and St. Paul Island, Alaska; Canadian Arctic Archipelago and the land adjacent; Gulf of St. Lawrence; Greenland; perhaps Iceland. Arctic-alpine grassland and tundra. Late June to early September.

Type collections: (1) *R. sulphureus*. The following is quoted from a letter from Dr. H. W. Rickett of the New York Botanical Garden: "No habitat or location given. But on p. 58 he mentions sending a party ashore on Low Island, off the coast of Spitzbergen, and quotes Dr. Irving thus: the ground was 'covered with moss, scurvy grass, sorrel, and a few ranunculuses then in flower.' Since this is the only mention of vegetation in the text, it is probable that *R. sulphureus* was collected then (July 29). The work on plants is often but rather groundlessly attributed to Solander. On pp. 12–13 of Introduction, Phipps acknowledges his indebtedness to Banks 'for his assistance in drawing up the account of the productions of that country.' If Solander had had a hand, he would have mentioned it. If specimens exist they should be in Brit. Museum." (2) *R. altaicus.* The following is quoted from Dr. Rickett: "Exclude from description reference to Tab. VII., which is an error for Tab. VIII. After the detailed description is the following: 'Circa finem Junii in alpium nivosarum planitie muscosa florenum inveni.' And in the abstract on p. 49 of same volume he says 'in fissuris praedictarum alpium umbrosis habitans.' Laxman lived, and presumably collected, in Kolivan, near the present Novosibirsk in the province of Zapadni. The Altai range begins about here. Note also the following introductory remarks: 'In describendis plantis sibiricis pergens, nunnullas illarum tantum nunc botanicis offerre volui, quas in summis altaicorum nontium aeterne nive tectorum cacuminibus legi, quaeque mihi maxime singulares visae sunt.' The type of *R. altaicus* would therefore come from alpine locations in the Altai mountains."

41. Ranunculus Macauleyi A. Gray, Proc. Am. Acad. **15**: 45. 1879.

Meadows in the mountains at 3,400 to 3,800 meters elevation; Rocky Mountain System in Southwestern and South-Central Colorado and Northern New Mexico. Arctic-alpine grassland. July.

Type collection: "Rocky Mountains in San Juan Co., Colorado, Lieut. C. H. McCauley, Mr. F. N. Pease." "McCauley collected 2 specimens . . . in the summer of 1877."

42. Ranunculus Grayi Britt. Bull. Torrey Club **18**: 265. 1891. *R. pedatifidus* Hook. Fl. Bor. Am. **1**: 18. *Pl. 8. f. B.* 1829, not J. E. Smith in 1819. *R. Hookeri* Regel, Reisen Ost-Sib. **1**: 47. 1861, not Schlect in 1834. *R. Drummondii* Greene, Erythea **2**: 192. 1894.

High peaks of the Rocky Mountains in Alberta (lat. 52°–55°, *Drummond*) and in Colorado (Gray's Peak, *Patterson* and at 13,000 feet elevation near Ironton, *S. H. Camp* in 1893.) The writer has seen only the Ironton specimen. Hooker's figure shows a plant with more deeply- and completely-dissected leaves and with sepals nearly as long as the petals. The apparent relationship is to *R. Eschscholtzii* Schlect. Arctic-alpine grassland. Summer.

Type collection: "Barren summits of the Rocky Mountains, on the eastern side of the ridge, lat. 52° to 55°, *Drummond.*" The later names are based on the same type.

43. Ranunculus pygmaeus Wahl. Fl. Lapp. 157. 1812.

Radical leaf blades simple, semicircular, 5–9 mm. long, 6–11 mm. broad, 3-parted or -divided, the middle lobe entire, the lateral 2–3-lobed, proximally truncate or nearly cordate and distally rounded in outline, petioles 1–3.5 cm. long, stipular leaf bases up to 1 cm. long; cauline leaves alternate or practically opposite, the bracts divided, sessile; achenes 40–50 in an ovoid or subglobose head 2.5–4 mm. long by 2.5–3 mm. in diameter.

Damp meadows and tundra at low elevations near the Arctic Sea and up to about 1,600 meters elevation in Alberta; circumboreal; Alaska to the Canadian Rockies; Ellesmereland to Labrador; Greenland; Spitzbergen. Arctic-alpine grassland. July to September.

43 A. RANUNCULUS PYGMAEUS var. PETIOLULATIS Fern. Rhodora **19**: 137. 1917.

Radical leaf blade divided, the divisions, sometimes shortly petiolulate, the middle division again 3-lobed, the lateral divisions 2- or 4-lobed or -cleft; head of fruits cylindrical, 5–7.5 mm. long and 3–4.5 mm. in diameter.

Damp, mossy hollows at 950–1,000 meters; Mt. Albert, Gaspe County, Quebec. Arctic-alpine grassland. August.

Type collection: "QUEBEC: damp mossy hollows in shade of amphibolite rocks, altitude 950–1000 m., Mt. Albert, Gaspe County, August 8 & 10, 1905, *Collins & Fernald*, no. 82 in large part (TYPE in Gray Herb.). . . . On Mt. Albert collections were made on two days at different points and all the material distributed under one number. The full sheet retained at the Gray Herbarium contains a few plants of true *R. pygmaeus*, but most of the specimens (presumably from a different station) are the variety."

44. RANUNCULUS RHOMBOIDEUS Goldie, Edinb. Jour. **6**: 329. 1822. (?) *Ranunculus ovalis* Raf. in Desv. Jour. Bot. **4**: 268. 1814, *nomen nudum*. *R. brevicaulis* Hook. Fl. Bor. Am. **1**: 13. 1829.

Prairies from Moose Jaw to Manitoba and Ontario and from the Dakotas to Michigan. Prairie grassland and northern coniferous and northeastern pine forests. March to May.

Type collections: (1) *R. ovalis*, "Canada." Many authors have attributed this name to *R. rhomboideus*, but there is little evidence that it was applied to that species, cf. Fern. Rhodora **38**: 175–7. 1936. (2) *R. rhomboideus*, "In dry sandy fields, near Lake Simcoe, Upper Canada [Ontario]." Collected by Goldie in Ontario County. (3) *R. brevicaulis*, "Shores of Lake Huron. *Dr. Richardson.* Drummond."

45. RANUNCULUS GLABERRIMUS Hook. Fl. Bor. Am. **1**: 12. *pl. 5. f. A.* 1829. *R. Austinae* Greene, Erythea **3**: 44. 1895.

Sandy soil in the sagebrush region at 300–1,700 meters elevation Northern Great Basin from British Columbia to Plumas County, California, and to Western Montana, and Western Colorado; Newell and Dickinson, South Dakota. Northern desert. April and May; the first flower of spring through much of its range. Both varieties are described in Abrams, Ill. Fl. Pac. Sts. vol. 2. (in press).

Type collections: (1) *R. glaberrimus*, "Common on the mountains around the Kettle Falls [Columbia River in Washington] and on the Rocky Mountains near the limits of perpetual snow. *Douglas.*" The Kettle Falls specimen is designated as a lectotype. (2) *R. Austinae*, "Crevices of lava rock east of Willow Creek Valley [Modoc County] in Northern California, Mrs. R. M. Austin, 1894. Species evidently allied to *R. glaberrimus*, though very distinct by its slender habit, snow-white petals, and elongated head of achenes." The petals of *R. glaberrimus*, like those of many other *Ranunculi*, turn white when they wither. The habit and head of achenes are normal for *R. glaberrimus*. A review of the Herbarium Greeneanum in 1935 failed to reveal the type specimen. ISOTYPES: *US 1466016, NY, UC.*

45 A. RANUNCULUS GLABERRIMUS var. ELLIPTICUS Greene, Fl. Fran. **1**: 298. 1892. *R. ellipticus* Greene, Pittonia **2**: 110. 1890. *R. Waldronii* Lunell, Am. Midl. Nat. **3**: 12. 1913.

Mountain meadows and the edge of the Great Plains at 1,500 to 3,000 meters elevation; from Lytton, British Columbia, through the Great Basin and Rocky Mountains to Truckee, California, western Montana, western South Dakota and Colorado; North Rim of the Grand Canyon, Arizona; Rio Arriba County, New Mexico. Western pine forest; plains grassland. April to June.

Type collections: (1) *R. ellipticus*, "Lower and Middle mountain districts of Colorado, Utah and Nevada to eastern California." Since there was only one California collection, the writer proposes it as a LECTOTYPE: Wet gravelly ground on road to Donner Lake [from Truckee] *C. F. Sonne*, May 16, 1886, *HGr 2583*. (2) *R. Waldronii*, "The type was collected on May 14, 1912, in a moist pasture at Dickinson, Stark County, in the southwestern part of this state [North Dakota] . . . named in honor of its first collector, Mr. Clarence H. Waldron. . . ." The TYPE was kindly sent to the University of Arizona for examination by Dr. C. O. Rosendahl of the University of Minnesota.

45 B. RANUNCULUS GLABERRIMUS var. RECONDITUS (Nels. & Macbr.) L. Benson, Am. Jour. Bot. **23**: 170. 1936. *R. triternatus* A. Gray, Proc. Am. Acad. **21**: 370. 1886. *R. reconditus* Nels. & Macbr. Bot. Gaz. **56**: 473. 1913.

Vernally moist slopes at 1,000–1,200 meters; Klickitat County, Washington, and near The Dalles, Oregon. Western pine forest (?). April and May.

Type collection: "Klickitat Co., Washington Terr., on high hills near Goldendale, *Howell*, by whom it has been distributed under the name of *R. Hookeri*." April 20, 1882.

Significant specimens, cf. L. Benson, Am. Jour. Bot. **23**: 170. 1936.

46. RANUNCULUS VERTICELLATUS Eastw. Bot. Gaz. **33**: 144. *f. 3.* 1902.

Known only from the type collection at Cape Nome, Alaska (fide type specimen). Arctic-alpine grassland. Summer.

Type collection: ". . . collected at Nome City during the flowering season of 1900." "Plants collected by Dr. F. E. Blaisdell at Nome City, Alaska."

47. RANUNCULUS JOVIS A. Nels. Bull. Torrey Club **27**: 261. 1900. *R. digitatus* Hook. Kew. Jour. **3**: 124. *pl. 4.* 1851, not Gilib. in 1781, not Willd. in 1842. *R. oreogenes* Greene, Pl. Baker. **3**: 2. 1901.

Moist ground of mountain meadows and near snowdrifts at 1,900–3,000 meters elevation; Fremont County, Idaho; Havallah Mountains, Nevada; northwestern Wyoming; Wasatch Mountains, Utah; Cerro, Southern Colorado. Northern coniferous forest. April to July, depending upon latitude and altitude.

Type collections: (1) *R. digitatus*, "Hab. in Rocky Mountains, near Fort Hall. *Mr. Burke*." (2) *R. Jovis*, "The type no. is 5817, collected on the Thunderer, Yellowstone Park, July 13, 1899, by Messrs. Elias Nelson & L. N. Goodding." (3) *R. oreogenes*, "at Cerro Summit above Cimarron, 7 June, no. 50," *C. F. Baker*. *HGr 2430*. The disposal of this species should be rechecked with the type.

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STUDIES IN THE GENTIANACEAE: GENTIANA, SECTION PNEUMONANTHE, SUBSECTION ANGUSTIFOLIAE

Robert T. Clausen

(WITH ONE FIGURE)

The plants known popularly as Pine Barren gentians constitute a natural subsection of the genus *Gentiana*. This group is characterized by the narrow leaves, the usually solitary flowers and the long corolla-lobes which far exceed the plaits and are either spreading or reflexed. The subsectional name, *Angustifoliae*, apparently introduced by Small (1933) without Latin diagnosis, may now be formally described as: Subsectio *Angustifoliae* Small, sectionis *Pneumonanthe*, generis *Gentiana*, foliis linearibus, floribus fere solitariis, lobis corollae longis, sinus multo excedentibus, aut expandentibus aut reflexis. Other species of the section *Pneumonanthe* have broader leaves and the corolla either cylindrical or, if infundibuliform, with the lobes more or less erect, not widely spreading.

KEY TO SPECIES OF SUBSECTION ANGUSTIFOLIAE

A. Stamens and pistil usually equaling the tube of the corolla at time of anthesis; corolla blue (rarely pink or white) dotted with green on inside of tube; plants tall, 1.5–4 dm. high .... 1. *G. porphyrio*

AA. Stamens and pistil one-half to two-thirds the length of the corolla tube at time of anthesis; corolla white dotted with green on inside of tube; plants relatively low, 1–3.6 dm. high, usually 2.5 dm. or less .... 2. *G. pennelliana*

1. GENTIANA PORPHYRIO J. F. Gmelin, Syst. Nat. ed. 13. **2**: 462. 1791.

Gentiana purpurea Walter (not Linnaeus, 1753), Fl. Car. 109. 1788. No type is extant. The original description designates the corolla as infundibuliform, lively purple within, the stem simple and the leaves linear. Except for the color of the inside of the corolla, this diagnosis fits the common Pine Barren Gentian. The color discrepancy is troublesome, but there seem to be two possible explanations for that. Walter may have had a specimen of the pink variety which is now known from southeastern North Carolina, or he may have based his notes on an herbarium specimen which had faded from blue to purple, as frequently happens in dried material. In any case, there is no other species of gentian, known from the Carolinas today, which has an infundibuliform corolla, truly linear leaves and a simple stem. Further, regarding the color, both Elliott (Sketch Bot. S. C. & Ga., **1**: 341. 1821) and Darby (Bot. So. St. p. 436, 1791), clearly referring to the same plant as that under discussion, stated that the corolla is blue tinged with purple. Since Gmelin's *G. porphyrio* is simply a new name substituted for Walter's *G. purpurea* because of the earlier homonym of Linnaeus, application of the epithet *porphyrio* must rest on interpretation of Walter's species.

Gentiana angustifolia Michx., Fl. Bor.-Am. **1**: 177. 1803. Described from meadows of lower Carolina and said to have narrowly linear leaves.

Dasystephana porphyrio (J. F. Gmelin) Small, Fl. S. E. U. S., 931. 1903.

Gentiana Stoneana Fernald, Rhodora **41**: 555. pl. 579. 1939. The TYPE specimen, in the Gray Herbarium, is illustrated in Rhodora. It is from a "siliceous and argillaceous thicket north of Factory Hill," Nansemond Co., Va., *Fernald and Long no. 9611*. Argument for this new name rests on the thesis that Walter's description, on which depends the application of *G. porphyrio* Gmelin, really applies to another species of which specimens are listed from Southampton Co., Va., Beaufort Co., S. C., and eastern N. C. Examination of this material indicates that the leaves are not linear, nor are the corollas truly infundibuliform. These plants belong to *G. parvifolia* (Nutt.) Britton, not to *G. purpurea* Walter. Although the flowers of the Pine Barren Gentian are distinctly funnelform, a fact attested by many authors, as Small (1933, p. 1052, 1054), Fernald wrote, "I find myself quite incapable of believing, when Walter described a plant with infundibuliform corolla lively purple within, that he referred to a plant with rotate azure- or indigo-blue flower." On this basis, Fernald renamed the species.

Slender perennial, 1.5–4 dm. high from a cluster of several fibrous roots which are 1–4 mm. thick; basal leaves narrowly elliptic, 1–4.5 cm. long, 6–7 mm. wide; cauline leaves linear, acute or obtuse, with the margins somewhat revolute, 0.7–6 cm. long, 1–4 mm. wide; flowers usually solitary and terminal, rarely two or three borne on pedicels in the axils of the upper leaves; calyx 2–3 cm. long, with the tube 0.8–1.2 cm. long and the lobes linear, acute, 0.8–2.3 cm. long; corolla funnelform, 3–5.5 cm. long with the tube 3.0–4 cm. long, greenish blue on the outside, blue spotted with green within; plaits lacerate, 3–6 mm. long, deep blue; lobes 1.0–1.5 cm. long, spreading or reflexed, deep blue, spotted with green below; stamens as long as the corolla tube; anthers yellow; pistil 2.5–3.5 cm. long; stigmatic lobes recurved, 2–5 mm. long. For an excellent description of the color of the flower, see the account by Pennell (1916).

Gentiana porphyrio is a plant of the Atlantic Coastal Plain, ranging from Monmouth County, New Jersey, to Florence, Florence County, South Carolina, and inland as far as Hartsville, Darlington County, South Carolina, Aberdeen, Scotland County, North Carolina and Fayetteville, Cumberland County, North Carolina. The characteristic habitat is in sandy pine barrens, where the plants may occur in situations ranging from the dry pine woods to moist peaty depressions. Data with one collection from near South Quay, Nansemond County, Virginia, indicate that the plants were growing there in hard gray clay.

Specimens seen:[1] Northernmost—pine woods, Monmouth Co., N. J., Torrey Herbarium (NY); easternmost—Manahawken, Ocean Co., N. J., *Bayard Long* (GH); westernmost—Hartsville, Darlington Co., S. C., *J. B. Norton 505* (US); southernmost—10 miles east of Florence, Florence Co., S. C., *A. N. Leeds 1622* (PH); oldest—Sept., 1814, Batsto, Burlington Co., N. J., ex herb. *F. J. Bumstead* (Corn); no. of collections seen—61.

The flowering time is earlier in the north and later in the south. From a study of data on herbarium sheets, extreme dates for flowering specimens in New Jersey are September 1 and October 28; in North Carolina, October 11 and December 15; and in South Carolina, October 25 and November 4. Probably flowers may be found in South Carolina much later than is indicated here, but at present few collections are available from that state.

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[1] Names of herbaria are abbreviated as: (Corn) Dept. of Botany, Cornell University; (GH) Gray Herbarium, Harvard University; (NY) New York Botanical Garden; (Ph) Academy of Natural Sciences of Philadelphia; and (US) United States National Herbarium.

The most notable variation is in the color of the flowers. These vary from deep blue to pink. I have seen the pink phase in the garden of Mrs. J. N. Henry, Gladwyne, Pennsylvania. These plants came originally from near Wilmington, North Carolina.

Information on the cytology and breeding relationships of this species is still lacking. The chromosome number should be determined for plants from various parts of the range, also for both typical and pink-flowered specimens. Genetical studies should include experiments to determine the degree of compatability with *G. pennelliana*.

According to Pennell (1916) the oldest illustration was published in 1758, in Edwards' "Gleanings of Natural History, vol. 5, 1.98." An excellent colored plate appeared in Addisonia, vol. 1, 1916, plate 35.

2. GENTIANA PENNELLIANA Fernald, Rhodora **42**: 198. 1940.

Gentiana alba Croom (not Muhl. 1813), Am. Jour. Sci. **25**: 69. 1833.

Diploma tenuifolia Raf., Flora Telluriana **3**: 27. 1836. The TYPE, at the New York Botanical Garden, was collected in Florida, in 1832, by Mr. Croom.

Dasystephana tenuifolia (Raf.) Pennell, Bull. Torr. Bot. Club. **46**: 183. 1919.

Gentiana tenuifolia (Raf.) Fernald (not Petrie, 1913), Rhodora **41**: 557. 1939.

Slender perennial, 1–3.6 dm. high, from a cluster of several fibrous roots which are 1–4 mm. thick; leaves linear or narrowly elliptic-linear, acute or obtuse, revolute, 0.5–3 cm. long, 1–3 mm. wide; flowers usually solitary and terminal, rarely two or three borne on pedicels in the axils of the upper leaves; calyx 1.7–3 cm. long, with the tube 0.7–1.0 cm. long and the lobes linear, acute, 1–2 cm. long; corolla 4.5–6 cm. long with the tube 3.5–4.5 cm. long, white dotted with green on inside, greenish white on outside; plaits lacerate, 3–10 mm. long, white; lobes 1.2–1.8 cm. long, ovate-elliptic, spreading, white; stamens one-half to two-thirds the length of the corolla-tube at time of anthesis; pistil 2.5–2.7 cm. long; stigmatic lobes slightly spreading, 1 mm. long.

Gentiana pennelliana is a plant of very limited distribution on the East Gulf Coastal Plain in western Florida, ranging from Wakulla County westward to Walton County and northward to Gadsden County. The habitat usually is moist places in low pine woods.

Specimens seen: Northernmost—low pinelands near Wetumpka, Gadsden Co., *J. K. Small et al. 10987* (NY); easternmost—flatwoods, Newport, Wakulla Co., *H. Kurz* (NY); westernmost—Point Washington, Walton Co., *C. D. Mell* (US); southernmost—Apalachicola, Franklin Co., *Biltmore Herbarium 467b* (GH, NY); oldest—1832, Florida, *Croom* (NY); no. of collections seen—21.

The flowering time, as determined from the data on herbarium labels, extends from late October to January. No noteworthy variations in the color of the corolla are known. In the herbarium, the flowers may become brownish.

As interpreted by the descriptive taxonomist, *Gentiana porphyrio* and *G. pennelliana* are distinct species with both morphological and geographical discontinuity. Genetical discontinuity must yet be demonstrated.

Illustrations: see figure 1.

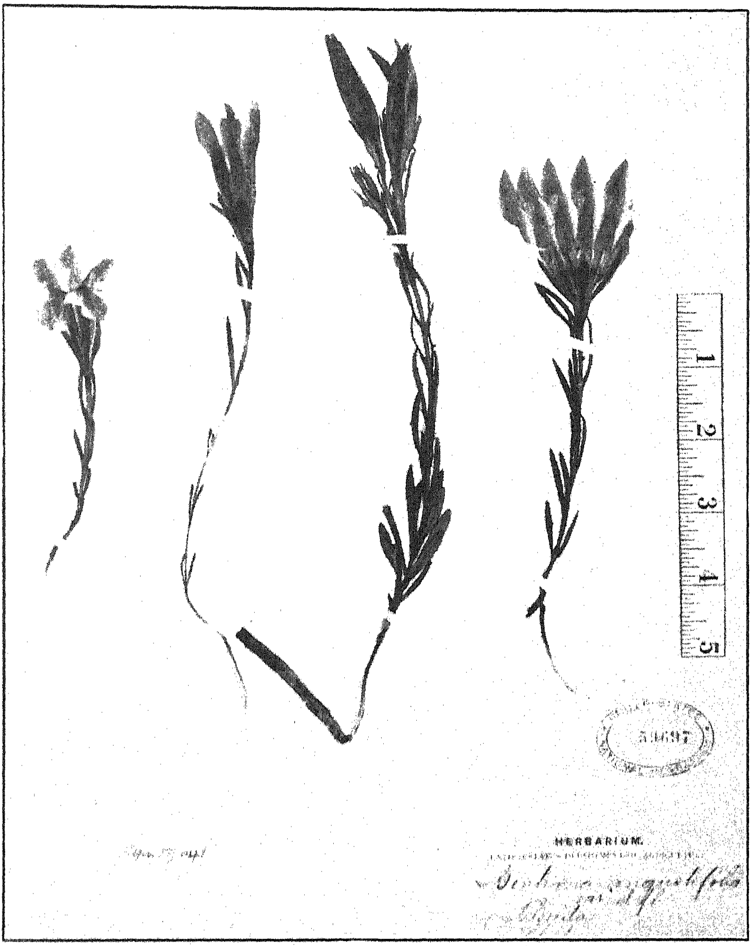

FIG. 1. *Gentiana pennelliana* Fernald. Specimens collected by Chapman in Florida. Sheet in U. S. National Herbarium, no. 59697.

SUMMARY

The Subsection *Angustifoliae* of *Gentiana*, Section *Pneumonanthe* contains two species which are distinguished by several characters. The proper name for the blue-flowered species is *Gentiana porphyrio*.

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Literature Cited

Pennell, F. W. 1916. *Dasystephana porphyrio.* Addisonia 1: 69–70, plate 35.

Small, J. K. 1933. Manual of the southeastern flora. New York, The Science Press Printing Co., p. i–xxii, 1–1554.

NOTE:—Since the above was written, the writer has observed in the pine barrens of New Jersey white-flowered plants of *G. porphyrio.* Rumors are also current of the pink-flowered phase in New Jersey.

THE SUCCESSFUL REVIVAL OF NOSTOC COMMUNE FROM A HERBARIUM SPECIMEN EIGHTY-SEVEN YEARS OLD

Charles B. Lipman

The author's interest in the longevity of microorganisms as indicated by a number of published studies has led him to search for old materials of appropriate kinds from many sources. Among other sources which appealed to him as interesting and useful for obtaining material of no great age, and yet of significant age and authentic dating, was herbarium material from the cryptogamic collections. Through the great kindness of Doctor Francis Drouet of the Field Museum of Natural History, it was possible for me to obtain specimens of several algae from such a collection. These algae were inoculated into sterile Detmer's solution in Erlenmeyer flasks. The cotton stoppers were protected from dust by paper caps. In most cases the material taken from the herbarium sheets was very scanty and it consisted of desiccated fragments or scales. In the period of more than two years during which the cultures were maintained on a table in the laboratory, only one culture, namely one of *Nostoc commune* Vauch., developed growth of new masses of the organism as will be related below. During the incubation of the cultures the temperature conditions were not controlled, but varied from night to day, and from season to season as is characteristic of a laboratory at Berkeley. The extremes of temperature to which the cultures were subjected were approximately from 14° C. to 30° C. The light was mostly that of indirect sunlight from a south window, but in the winter months was supplemented by light from a 100-watt lamp during most of the day and night.

The specimen of *Nostoc* which was revived and produced vigorous new growth was derived from the collection of H. Royers, now a part of the collections of the Cryptogamic Herbarium of the Field Museum of Natural History. The label on the original specimen is as follows:

Nostoc commune Vauch
Germany: Zwischen Naumburg und den Sperlingsholze,
Preussen. 26 Juni 1853.
C. Schliephacke

From the material of this specimen donated by Dr. Drouet the first culture was prepared on the 1st April 1939. A small amount of the material was used in this culture, the balance being reserved for later inoculations. Growth was first noted in this culture on the 15th October 1939. This growth manifested itself by the appearance of dots of green on the original material and these green dots always showed bubbles of gas presumably oxygen from photosynthesis. It is worthy of emphasis that it was always directly from the old material that the green dots and the gas bubbles arose. Microscopic examination showed typical cells and other structures of *Nostoc commune*. The long period of exposure of the original *Nostoc* material to the culture solution before growth developed is particularly noteworthy and seems to be characteristic as will be shown below. The result obtained with the first inoculation thus indicates that *Nostoc commune* may be revived after remaining in a desiccated state on a herbarium sheet for eighty-six years. This conclusion need not be allowed to rest on one observation alone, however, as the following discussion renders clear.

A second inoculation from the same source of *Nostoc* material was made on the 20th July 1939 with exactly the same technique as that employed in the first inoculation. In this culture the first growth noticed was on the 1st June 1940 or about ten months after the inoculation was made. Again the first evidence of growth manifested itself by the appearance of small dark green dots or tiny patches on the old material, and gas bubbles were easily discernible.

When the second culture developed growth, I decided to try a third inoculation. This was done on the 13th July 1940. On the 4th February 1941 growth was first noted in this culture. Microscopic examination in this as in the first and the second cultures showed typical *Nostoc commune* cells and chains of cells. This third culture proves moreover that the dried *Nostoc* material may withstand desiccation for eighty-seven as well as eighty-six years. How much longer such material can withstand desiccation and other untoward conditions on a herbarium sheet can of course only be ascertained by continued experiments of this kind with the original herbarium material as long as that can be spared.[1]

Of the other algal specimens tested by the same technique none have as yet shown signs of life. These algae included other and older specimens of *Nostoc* as well as other forms of blue-green and of green algae. In this regard, however, it is important to note that there is very little, if any, information at hand relative to the treatment which different specimens in the same herbarium received. For example, if fumigation or other methods of preservation had been employed, the specimens can hardly have survived in living form, unless the poisoning technique had been ineffective. It is doubtless true that some specimens of cryptogams had not been subjected to poisons at all, whereas others may have been treated drastically. In other words negative results such as those mentioned above remain under the circumstances indecisive, relative to the longevity of the algae, whereas a positive result such as the one here reported for *Nostoc* is clearly decisive.

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[1] Since this paper was sent to the printer, a fourth culture of *Nostoc,* made from the same herbarium specimen, has developed good growth after an incubation period of nearly five months. In addition, a culture of *Anabaena oscillarioides* from a specimen 74 years old has after an incubation of nearly two years just begun to show characteristic cells and chains of cells.

The writer's search of the literature does not reveal thus far any cases of greater longevity for algae than the one reported above. Certain seeds have, however, been shown to possess greater longevity. For example, the viability of *Nelumbium* seeds at the Kew Gardens after one hundred and fifty years, and of seeds of four or more orders in Paris after one hundred and fifty-eight years as reported by Becquerel are well known and decisive so far as they go.[2] The reports of Ohga regarding viability of seeds of *Nelumbium* from a peat bog in Manchuria after an estimated four hundred years of inactivity are also to the point but not decisive because of the uncertainty in the estimate of the age of these seeds. All these observations are in striking contrast to those which I have published on the longevity of bacteria, which appear, at least in some instances, to live indefinitely in a state of suspended animation. Of course, the observations on algae are still quite fragmentary and therefore do not make as satisfactory a comparison with those on bacteria as we should have. But the observations on seeds are in another category. They indicate quite strongly that seeds do not survive the ravages of time and untoward conditions nearly as well as bacteria. This subject, however, will be discussed more fully elsewhere. As regards the comparison of algal material and seeds, it may be remarked that the latter would seem to have the advantage over the former in resisting desiccation and other untoward conditions by reason of the protection to the embryo furnished by the seed. Such protection is especially great for example in the case of *Nelumbium*. The bits of algal material in a herbarium specimen on the contrary are completely exposed to the forces of the environment.

SUMMARY

Nostoc commune Vauch., from a herbarium specimen, has been revived and made to grow luxuriantly in culture solution eighty-six and eighty-seven years after it had been collected and placed in the herbarium.

THE UNIVERSITY OF CALIFORNIA
BERKELEY, CALIFORNIA

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[2] See the excellent review by J. H. Turner, Kew Bull. **1933**: 257–268.

BREEDING WORK TOWARD THE DEVELOPMENT OF A TIMBER TYPE OF BLIGHT-RESISTANT CHESTNUT: REPORT FOR 1940[1]

ARTHUR HARMOUNT GRAVES

(WITH ONE FIGURE)

The season of 1940 was the poorest for effective cross pollination of the chestnut that we have experienced since we began the work in 1930. The spring was abnormally cold, and continued so into the month of July.[2]

The cold weather had the following important effects:

1. Flowering was delayed. Usually, with some exceptions, all species and hybrids have finished blooming at the Hamden (Conn.) Plantation by July 15. (Of course, with the everblooming *Castanea Seguinii* and some of its hybrids, flowering often continues up to frost.) But in 1940 some Japanese-American and other hybrids were still in flower on August 1, and a few Chinese trees (*C. mollissima*) were still in their prime at this date.

2. The above statement applies to those flowers that matured. Apparently on account of the cold, some of the pollen bagged for crossing never matured, and many of the pistils bagged for crossing dropped off in the bags, both before and after pollination.

3. After crossing, fertilization did not result as regularly as usual. Many burs developed parthenocarpically, containing no embryos. It is possible that the unusual dryness of August and September played some part in this. We should bear in mind that only a comparatively short time is available for the chestnut to develop its fruit and ripen its seeds, as compared with the much longer period that oaks and hickories have.

POLLEN RECEIVED IN 1940

Pollen of the chestnut was received toward the end of June and in early July, from several institutions or persons whose cordial cooperation we take pleasure in acknowledging. Lack of space prevents us from including all their names in this report.[3]

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[1] Brooklyn Botanic Garden Contributions, No. 95. For a statement of the purposes and a brief review of the work, see Bull. Torrey Club **67**: 773–77. 1940. Recent annual reports have been published in the Brooklyn Botanic Garden Record, as follows: for 1936, **26**: 47–60; for 1937, **27**: 44–55; for 1938, **28**: 52–60; for 1939, **29**: 58–63; for 1940, **30**: 87–92.

[2] The records at the U. S. Weather Bureau in New York City give the minimum temperature on July 4, 1940, as 58°. This was the same as the maximum temperature on December 25, 1940, namely, 58°; literally, as "cold as Christmas."

[3] The complete list of donors of pollen in 1940 appears in the Annual Report of the Brooklyn Botanic Garden for 1940, Brooklyn Bot. Gard. Record **30**: 88, 89.

The source of the pollen received from the Stark Bros. Nurseries, at Louisiana, Missouri, is of such general interest that we shall state it briefly here. In the settling of the estate of Mr. Luther Burbank, the Stark Bros. Nurseries took over various plant material there. But I shall let their letter speak for itself:

> "When we took over the Burbank grounds there were about 500 chestnut trees in one row. They have since been cut down since Mrs. Burbank is using the ground. However, before taking them out we selected some of the most vigorous seedling trees and transferred them here to our grounds in Missouri. As a result we have about 10 trees here which are about 8 years old at this time. I have selected about 5 of these trees as the most vigorous in the lot and the catkins you received are from these trees. We will be interested in hearing of any results you obtain.
>
> "Assuring you I am glad to be of service, I am
>
> Sincerely yours,
>
> (Signed) Glenn Thomas
> Special Service Department
> Stark Bros. Nurseries"

Earlier in the letter Mr. Thomas has this to say in response to a question on the pedigree of the trees bearing the pollen:

> "I have been going through some of the records which we have here and I find that back in 1884 Mr. Burbank imported some Oriental chestnut seedlings from Japan and some European seedlings from Italy, and at the same time obtained some samples of chestnuts from the eastern United States and also some Chinquapins. According to the records these sorts were all hybridized back and forth in such a way that Mr. Burbank said all of his chestnuts had a most complicated ancestry. I find in the records that at first he was chiefly interested in getting from these crosses a hybrid which would produce a large, sweet nut, also a tree which would grow fast and bear young. Then when the chestnut blight became an important factor in the east Mr. Burbank's records indicated that he found 'hybrids of certain Oriental strains which appear immune to chestnut blight.' How he arrived at this conclusion I do not know, except that some of his hybrids may have been sent east for testing. I do not believe at this time there was any chestnut blight anywhere near California.
>
> "Mr. Burbank's records state that he found crosses between the Oriental Chestnut trees from Japan and our native Chinquapins were the most resistant to chestnut blight. No doubt his later breeding experiments were concentrated on these crosses."

We made many crosses with this Burbank pollen, but the most important was a cross on our most resistant Japanese, from which we obtained 5 nuts.

HYBRIDS OF 1940

As a result of the season's work we harvested 401 nuts, as against 767 in 1939 and 930 in 1938. Twelve of the combinations from which we obtained nuts are new to science, making a total of 48 new hybrid combinations made since we began this work in 1930.

Table 1 contains the list of the hybridizations in 1940 and the number of nuts resulting. All the hybridizing work was done on the trees on our own plantation at Hamden, Connecticut. As usual, the name of the female parent is given first. Those combinations which are new to science are preceded by an asterisk. The numbers at the left, in parentheses, correspond with the numbered notes which follow.

TABLE 1

Hybrids of 1940

		No. of Nuts
(1)	*Castanea crenata* × "Burbank"	15
(2)	*C. crenata* × *C. dentata*	47
	C. crenata × *C. floridana*	3
(3)	*C. crenata* × *C. pumila*	6
(4)	*C. crenata* × (*C* × *D*)[1]	15
(5)	*[*C. crenata* × (*C* × *D*)] × [(*C. mollissima* × *C. Seguinii*) × *C. crenata*]	1
(4)	(*C* × *D*) × *C. crenata*	8
	*(*C* × *D*) × *C. floridana*	1
(6)	(*C* × *D*) × (*C* × *D*)	39
(7)	*(*C* × *D*) × [(*C* × *D*) × *C. dentata*]	8
(8)	*(*C* × *D*) × [(*C* × *D*) × (*C* × *D*)]	51
(9)	*[(*C* × *D*) × (*C* × *D*)] × (*C* × *D*)	1
(10)	(*C. crenata* × *C. mollissima*) × *C. dentata*	19
	(*C. crenata* × *S8*[2]) × *C. dentata*	3
(11)	*C. dentata* × *C. crenata*	5
(12)	*C. dentata* × *C. mollissima*	10
(13)	*(*C. dentata* × *C. mollissima*) × (*C* × *D*)	2
(14)	(*C. dentata* × *S8*) × *C. crenata*	3
(15)	*(*C. dentata* × *S8*) × *C. mollissima*	32
(16)	*(*C. dentata* × *S8*) × (*C. crenata* × *S8*)	6
(17)	*(*C. dentata* × *S8*) × [(*C* × *D*) × *C. dentata*]	4
(18)	*C. mollissima* × *C. dentata*	32
(19)	*C. mollissima* × (*C* × *D*)	38
	(*C. mollissima* × *C. Seguinii*) × *C. dentata*	2
	(*C. mollissima* × *C. Seguinii*) × (*C. mollissima* × *C. Seguinii*)	20
	S8 × *C. mollissima*	1
	* *S8* × *C. neglecta*	3
(20)	(*S8* × *C. crenata*) × *C. dentata*	16
	*(*S8* × *C. crenata*) × *C. neglecta*	1
	(*S8* × *C. crenata*) × (*S8* × *C. crenata*)	3
	(*S8* × *C. crenata*) × (*C. crenata* × *S8*)	1
	*(*S8* × *C. dentata*) × (*C. mollissima* × *C. Seguinii*)	2
	C. Seguinii × *C. dentata* clone "Everbearing"	3
	Total	401

* *C* × *D* = *C. crenata* × *C. dentata*.

S8, one of the Van Fleet hybrids, is apparently a combination of *C. crenata* and *C. pumila*. The S8's in our plantation are from open pollinated seedlings of S8.

(1) This includes the cross with the Luther Burbank pollen mentioned in the text.

(2) We try each year to make more combinations of disease-resistant

Japanese and *dentata*. Most of the crosses this year we made on our Folk Japanese seedlings of 1930 (fig. 1), using *dentata* pollen sent us by Messrs. E. J. Grassman, from Elizabeth, N. J.; J. C. McDaniel, from Tennessee; Dr. G. A. Zimmerman, from Linglestown, Penn.; and Joseph St. John, from Monroe, N. Y.

(3) This cross was made with the purpose of finding out experimentally what is the composition of Dr. Van Fleet's hybrid "88." This has generally been supposed to be the result of a cross of *C. crenata* and *C. pumila*. This year was the first time that *C. pumila* has bloomed at our plantation, the plants having grown from nuts sent us in the fall of 1935, by Mr. R. B. Clapper of the Division of Forest Pathology, from the U.S.D.A. nurseries at Bell, Maryland.

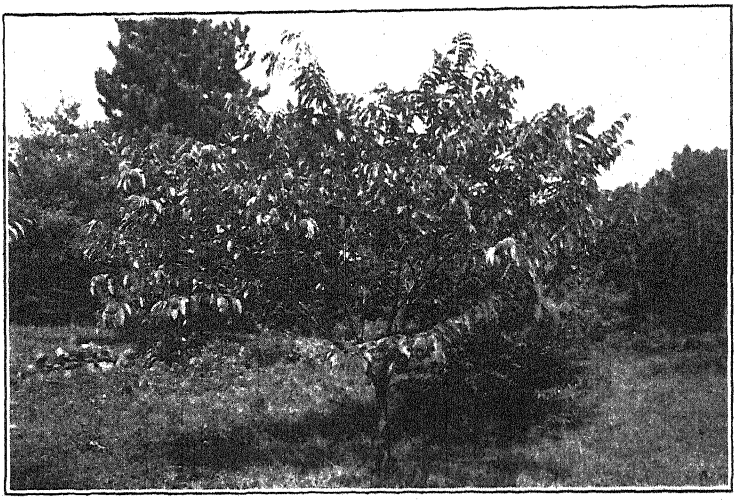

FIG. 1. *Castanea crenata*, 10 years old, and (according to results of inoculations) entirely disease resistant. Note low, bushy growth characteristic of the species, also good crop of large burs. Some of these are the result of crossing with the Burbank pollen.

(4) A cross of one of our Hammond Japanese-Americans (134 A 31) with our most disease-resistant Folk Japanese.

(5) This rather complicated cross represents two young hybrids (in brackets) which bloomed for the first time in 1940, at the age of three years.

(6) Represents a continued effort to get a good supply of F 2's by crossing together many Japanese-Americans.

(7) The pollen parent in this combination has grown from one of the first nuts we secured from crossing our Japanese-Americans. The first of these bloomed in 1934, at the age of three years. This was crossed with *dentata* pollen, received from the Division of Forest Pathology, U.S.D.A., at Washington, D. C. One of the trees resulting from this cross, namely, the pollen parent referred to above, bloomed this year at the age of six years, but with only staminate flowers.[4] These were used to pollinate one of our good Japanese-American hybrids—a cross of a Japanese owned by the late

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[4] For a photograph of this hybrid, see Brooklyn Bot. Gard. Record 30: 65. 1941.

Mr. Beekman Winthrop, of Old Westbury, Long Island, and *C. dentata* from Washington, D. C., made by us in 1931. The resulting nuts from this cross represent a new combination.

(8) The same Winthrop Japanese-American crossed with pollen from an F 2 Japanese-American, resulting from a cross of two Smith Japanese-Americans in 1936 and blooming this year for the first time. This cross gave a particularly fruitful yield—about ⅛th of our entire crop.

(9) The reciprocal of the last, but here the pistil parent was young (3 years) and only one nut resulted.

(10) The pistil parent here is habitually a very late bloomer, given to us by the Division of Forest Pathology, U.S.D.A., in 1932. Pollen of *dentata* from wild trees was sent to us by Mr. Philip Smith, of Pawling, N. Y., arriving as late as July 19, in most years too late to be of service. But in this unusually late season this Japanese-Chinese hybrid was in its prime at this date; hence the cross produced a good yield.

(11) The *dentata* parent is the same as that mentioned in my report for 1939.[5] This year, obviously very nearly at the end of its life, it had many pistillate flowers which were crossed with our most resistant Japanese, but only five nuts were gathered.

(12) As was done last year, the American parent just mentioned (note 11) was crossed with our most resistant Chinese.

(13) The pistil parent is the result of a cross of wild *dentata* trees at Half Hollow Hills, in the township of Huntington, Long Island, N. Y., using pollen of *C. mollissima* sent from our Hamden plantation in 1935. It was part of an effort made that year to see if by using as the female parent the American chestnut, instead of the Japanese or Chinese, as we had always done before, any difference in the character of the offspring would result. As far as we can determine, the character of the female parent makes no difference in this cross. The *dentata* stock is incompletely dominant in both cases. The American-Chinese hybrid was, therefore, five years old in 1940 and was crossed with one of our best Japanese-Americans, the latter being the result of a cross of a Japanese chestnut on the estate of Mr. John Minturn, Oyster Bay Cove, Long Island, with *dentata* pollen. That Japanese tree is still in fine condition and is one of the best now living in the region of New York City. Only two nuts were secured from the cross this year, but since the cross includes so many good elements it will be tried again next year.

(14) The pistil parent is the result of a cross on the native chestnut shoots at Half Hollow Hills, Huntington, L. I., in 1935, using S8 pollen from our plantation. The hybrid was crossed this year with pollen from one of our best Japanese trees; for we have learned that the S8's in our plantation, although precocious and prolific, are not as disease resistant as could be desired.

(15) Another *dentata* × *S8* resulting from a Long Island cross (see notes 14 and 13, also report for 1935[6]). This hybrid bloomed for the first time in 1938. This year it was crossed with one of our best mollissimas, with splendid results. The nuts have a promising pedigree.

(16) Another *dentata* × *S8*, with a history like that of the preceding, crossed with a 1935 hybrid of a good Japanese and *S8*. The Japanese grew

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[5] Bull. Torrey Club **67**: 775, note 5.

[6] See Brooklyn Bot. Gard. Record **25**: 66, 67.

from a nut obtained from the vicinity of Kyoto, Japan, through Dr. G. M. Reed, of the Brooklyn Botanic Garden, in December, 1931.[7]

(17) A fourth *dentata* × *S8*, with a history similar to that of the preceding three—this one crossed with the hybrid resulting from the back cross of Japanese-American with *dentata*, described in note 7.

(18) Resistant *mollissima* crossed with some *dentata* pollen sent us by Dr. G. A. Zimmerman, from Linglestown, Penn., through Miss Hilda Vilkomerson, and also by Mr. Joseph St. John, from Monroe, N. Y.

(19) This represents a continued effort to incorporate more of the resistance of the mollissima stock with the Japanese-American hybrids.

(20) *S8* × *C. crenata* contains no *dentata* in its constitution. It is fairly disease resistant; hence this cross with *C. dentata*. The *dentata* pollen used came from Elizabeth, N. J., sent by Mr. E. J. Grassman.

COOPERATIVE PLANTINGS

Because our own available land at Hamden, Connecticut is now fairly well stocked with species and hybrids, we are extending our plan of establishing cooperative plantations on land of responsible persons interested in bringing back the chestnut tree to North America. The trees growing in the first three of these cooperative plantations are listed in our 1939 report, but plantations are now too numerous even to name here. During 1940 we distributed more than 1500 seedlings in New Hampshire, Massachusetts, Connecticut, New York State, and New Jersey. In cases where particularly valuable hybrids have been distributed, the owners are required to sign the following statement:

> The undersigned agrees to grow this material for test purposes only, and further agrees not to propagate, sell, give away, or otherwise distribute the material until authorized to do so by Arthur H. Graves, Brooklyn Botanic Garden, Brooklyn, N. Y.

The area planted to trees is thus increased many times, so that the total number of trees growing is far larger than we could handle on our own plantation. As all plant breeders know, large numbers increase the chances of success, when a definite object is to be realized through breeding. Further, by this method of extension plantation, the trees are tested in a variety of soils and sites which we alone could not furnish.

VARIATION IN CASTANEA DENTATA

The chestnut, as a genus, shows a considerable amount of variability, and this character is shared by the different species.[8] For example, in the American chestnut, the qualities of the nuts varied so much that local forms received special names.[9] The European chestnut (*C. sativa*) and the Japanese (*C. crenata*) also show a wide variation in the size and quality of the nuts.

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[7] Brooklyn Bot. Gard. Record 25: 68, notes 11, 12.

[8] Darwin, Francis. The foundations of the origin of species, two essays written in 1842 and 1844, by Charles Darwin. p. 83, Univ. Press, Cambridge, 1909. "In many species the variability of certain organs or qualities is even stated as one of the specific characters."

In the summer of 1918, when we made a survey of the American chestnut trees then growing in the New York City region, a large amount of variation was shown in the amount of disease resistance manifested by different individuals,[10] another evidence of the variability of the species.

Now we are confronted with a situation extending over the whole range of the native chestnut tree, characterized by a succession of young shoots arising from the stumps (or bases) of diseased and dead trunks. These shoots develop for a few years, but are at length penetrated by the blight fungus. This condition is due to the fact, as we have learned,[11] that the roots of the trees are more resistant to the attacks of the fungus than is the trunk or its branches.

This continued development of a very large number of new shoots from adventitious buds offers abundant opportunity for bud variation to occur. I believe that such variation should occur with greater frequency, or intensity, or both, in these basal shoots than in the ordinary branches developing from normal buds. However, there seems to be scant evidence in the literature in support of this belief, perhaps because of the unusual nature of the situation. Beyerinck,[12] however, as a result of pruning *Cytisus Adami,* obtained segregation in the shoots developing from dormant buds, showing an unstable chromosomal condition resulting from such treatment. The killing of chestnut trees to the base by the blight fungus and the subsequent development of shoots from adventitious buds seems to be a similar situation. In any case, however, this continued production of basal shoots in all probability entails a certain amount of bud variation, for this phenomenon is likely to occur even under normal circumstances; and it is entirely probable that some of this bud variation will be along the line of greater disease resistance. The fact that many of these young chestnut shoots seem to be living longer and getting larger than formerly may be due to just this situation, i.e., to bud variation in the direction of disease resistance.

Now, it is fortunate that many of these basal shoots live long enough to flower and bear nuts. The qualities developed through bud variation, if they are hereditary, may be represented in these embryos.

It is on account of the above reasoning that we are trying to obtain as many nuts as possible of wild American trees or shoots of *C. dentata.* At present we have growing on our plantation at Hamden, Connecticut, more than 100 young trees of *Castanea dentata.* These Americans have been grown during the past fifteen years from nuts obtained from many of the states where *Castanea dentata* is native. They are being tested for disease resistance. If the results are favorable they will be used for breeding stock. Last fall we received nuts from interested persons in the following States: Massachusetts, Rhode Island, Connecticut, New York, New Jersey, Pennsylvania, and Kentucky.[13]

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[9] Corsa, W. P. Nut Culture in the United States. U.S.D.A. Div. of Pathology, unnumbered bull., 1896. p. 88.

[10] Graves, A. H. Resistance of the American chestnut to the bark disease. Science **48:** 652, 653. 1918.

[11] Graves, A. H. The cause of the persistent development of basal shoots from blighted chestnut trees. Phytopathology **16:** 615–621. 1926.

[12] De Vries, Hugo. The mutation theory, Vol. II, p. 626. 1910.

We find that the best method of handling the nuts is to plant them immediately after gathering. If any nuts are to be mailed to us, they should be wrapped in damp sphagnum moss, moist cotton, or paper napkins, to prevent drying out. A few days in a heated room may be fatal, for drying kills the embyro. Any nuts sent us will be planted immediately in our cold frames at the Garden and labelled with the name of the sender and the locality of the parent tree. Address: Arthur H. Graves, 1000 Washington Avenue, Brooklyn, New York.

Acknowledgment. We are glad to have this opportunity to express our indebtedness to the many individuals and institutions, and especially to the Division of Forest Pathology, U.S.D.A., for their cordial cooperation with us in our project.

BROOKLYN BOTANIC GARDEN
BROOKLYN, NEW YORK

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[13] See Brooklyn Bot. Gard. Record **30**: 91, 92. 1941.

MISCELLANEOUS TAXONOMIC NOTES

HAROLD N. MOLDENKE

Continued routine identification work in the herbarium of the New York Botanical Garden has revealed the desirability of a number of transfers from the genus *Polygonum* to the genus *Reynoutria* (formerly known under the name of *Pleuropterus*) and has brought to light two as yet undescribed species of *Peiranisia* and *Byrsonima* from Cuba.

Reynoutria Auberti (L. Henry) Moldenke, comb. nov. *Polygonum Auberti* L. Henry, Rev. Hort. **1907**: 82–83. 1907.

Reynoutria baldschuanica (Regel) Moldenke, comb. nov. *Polygonum baldschuanicum* Regel, Act. Hort. Petrop. **8**: 684, *pl. 10.* 1884.

Reynoutria campanulata (Hook. f.) Moldenke, comb. nov. *Polygonum campanulatum* Hook. f., Fl. Brit. Ind. **5**: 51. 1886.

Reynoutria ciliinervis (Nakai) Moldenke, comb. nov. *Polygonum ciliinervis* Nakai in Fedde, Repert. **13**: 267–268. 1914.

Reynoutria japonica var. **compacta** (Hook. f.) Moldenke, comb. nov. *Polygonum compactum* Hook. f. in Curtis, Bot. Mag. **106**: *pl. 6476.* 1880.

Reynoutria japonica var. **spectabilis** (de Noter) Moldenke, comb. nov. *Polygonum cuspidatum* var. *spectabile* de Noter, Rev. Hort. Belg. **35**: 232–234. 1909.

Reynoutria lichiangensis (W. W. Sm.) Moldenke, comb. nov. *Polygonum lichiangense* W. W. Sm., Notes Bot. Gard. Edinb. **8**: 197. 1914.

Reynoutria multiflora (Thunb.) Moldenke, comb. nov. *Polygonum multiflorum* Thunb., Fl. Jap. **1**: 169. 1784.

Reynoutria polystachya (Wall.) Moldenke, comb. nov. *Polygonum polystachyum* Wall., Numer. List 46, no. 1686, hyponym (1829), Pl. As. Rar. **3**: 61. 1832.

Reynoutria Spaethii (Damm.) Moldenke, comb. nov. *Polygonum Spaethii* Damm., Notizbl. Bot. Gart. Berlin **2**: 378. 1899.

Reynoutria Weyrichii (F. Schmidt) Moldenke, comb. nov. *Polygonum Weyrichii* F. Schmidt in Maxim., Prim. Fl. Amur. 234. 1859.

Peiranisia Bucherae Moldenke, sp. nov. Frutex vel arbor; ramulis gracilibus minute puberulis glabrescentibus; nodis valde abbreviatis; foliolis 6 vel 8 coriaceis utrinque pernitidis ellipticis, ad apicem rotundatis emarginatis, ad basim acutis, integris revolutis utrinque glabris vel parce pilosulis; glandulis 3.

Shrub or tree; branchlets slender, gray, minutely puberulent when young, soon glabrescent; nodes greatly abbreviated; leaf-scars large, horizontally oblong, with prominent margins; leaves alternate, evenly pinnate-compound with 3 or 4 pairs of leaflets; leaflets coriaceous, rather grayish green and very shiny on both surfaces, elliptic, 1.2–3.9 cm. long, 0.5–1.7 cm. wide, rounded and emarginate at apex, acute at base, entire and revolute along the margins, glabrous on both surfaces or with few scattered pilosulous hairs at the base; petiolules stout, about 1 mm. long, glabrous or very obscurely pilosulous-puberulent; gland circular, about 1 mm. in diameter, one between each of the 3 upper pairs of leaflets; rachis angular-costate, glabrous or very obscurely and minutely scattered-pilosulous; pedicels slender, 2.5–3 cm. long, very sparsely scattered-pilosulous with minute hairs; sepals

5, heavy, unequal, suborbicular, 3–6 mm. long and wide, rounded at both ends, venose, glabrous or the smaller ones microscopically pilose; petals yellow, large, irregular, unequal, 9–13 mm. long, 5–9 mm. wide, very venose, glabrous, the margins crisped; stamens 10, beakless; filaments about 1.4 mm. long, glabrous; anthers oblong, about 3 mm. long and 1.4 mm. wide; ovary elongate, flattened, 6 mm. long or longer, appressed-sericeous; immature legume flattened, elongate, 4 cm. long, with a minute circular disk on the very apex of the narrowed point, the valves thick-margined, glabrate.

CUBA—ORIENTE: Moa, *Mrs. George Conrad Bucher 78*, TYPE; in the Britton Herbarium at the New York Botanical Garden. The specimen was examined by my good friend, E. P. Killip, who was not able to place it in any known Cuban species.

Byrsonima Bucherae Moldenke, sp. nov. Frutex; ramis ramulisque adpresso-tomentellis glabrescentibus; nodis valde annulatis subarticulatis; hornotinis densissime ferrugineo-tomentellis; petiolis crassiusculis dense ferrugineo-tomentellis canescentibus; laminis coriaceis, supra nitidis, anguste ellipticis vel elliptico-lanceolatis, ad apicem angustatis emarginatis, ad basim acutis vel obtusis, integris revolutis, subtus dense ferrugineo-farinaceis.

Shrub; branches and branchlets slender, gray, very closely appressed-tomentellous, glabrescent in age; nodes conspicuously annulate, subarticulate; twigs very densely ferruginous-tomentellous when young; leaves decussate-opposite; petioles stoutish, flattened above, densely ferruginous-tomentellous, the tomentum more appressed, incanous, and less obvious in age; blades coriaceous, gray-green and shiny above, ferruginous or brunneous beneath, narrow-elliptic or elliptic-lanceolate, 2.4–5.8 cm. long, 0.6–2.1 cm. wide, regularly narrowed to a narrow and slightly emarginate apex, acute or obtuse at base, entire and revolute along the margins, ferruginous-farinaceous above when immature, glabrate or subglabrate when mature, very densely ferruginous- or brunneous-farinaceous beneath; midrib slender, deeply impressed above, very prominent beneath; secondaries slender, 4–8 per side, short, divergent, conspicuously arcuately joined some distance from the margins, impressed above, sharply prominent beneath; veinlet reticulation abundant, impressed above, prominulous beneath; pedicels slender, about 2 cm. long, longitudinally costate, very densely ferruginous-tomentellous; receptacle long-villous; sepals ovate, densely ferruginous-tomentellous, the acuminate free portion recurved and revolute, with a pair of oblong basal glands about 1.5 mm. long at the base; petals 5, long-clawed, the stalk about 3 mm. long, glabrous, canaliculate above, the blade obcordate, about 5 mm. long and 5.1 mm. wide, irregular-margined; stamens 10, erect, close together; filaments about 2.5 mm. long, glabrous; anthers 2-celled, oblong, about 0.7 mm. long, the connective prolonged into a spur-like projection about 1–1.3 mm. long, glabrous; pistil 1; ovary ovate, about 1.7 mm. long, glabrous; styles 2, about 3 mm. long, glabrate.

CUBA—ORIENTE: Moa, *Mrs. George Conrad Bucher 57*, summer of 1939; in the Britton Herbarium at the New York Botanical Garden; named in honor of the collector. My good friend, C. V. Morton, recognized expert on this group, says of it "*Byrsonima* prob. sp. nov. aff. *B. Wrightiana* Urb. & Ndzu."

THE NEW YORK BOTANICAL GARDEN

INDEX TO AMERICAN BOTANICAL LITERATURE

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

Papers that relate exclusively to bacteriology, forestry, agriculture, horticulture, manufactured products of vegetable origin, or laboratory methods are not included. If users of the Index will call the attention of the editor to errors or omissions, their kindness will be appreciated.

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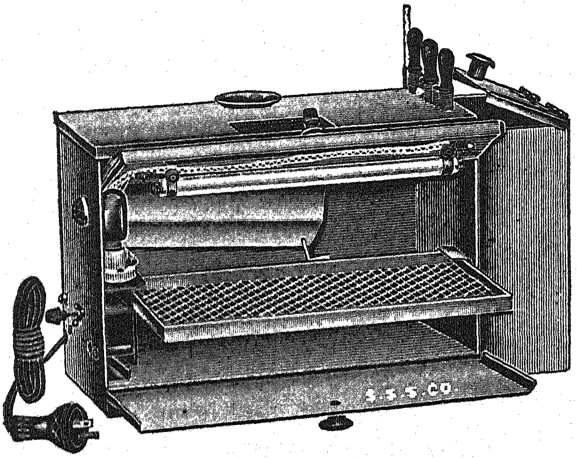

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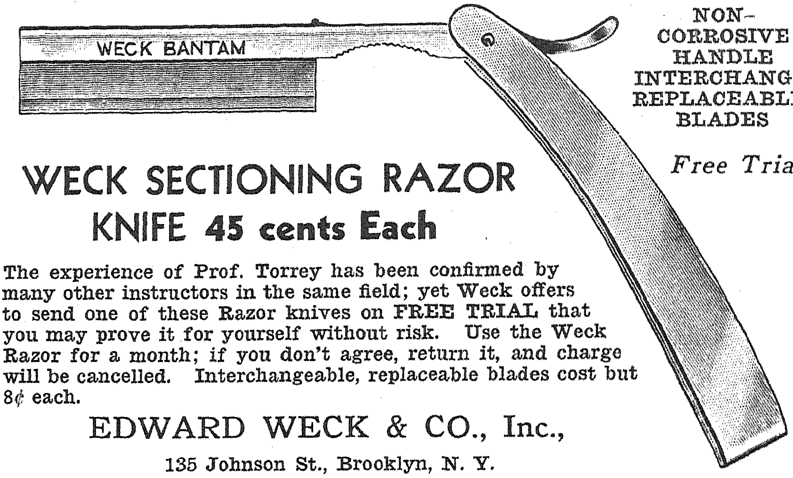

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